Journal OF THE Fisheries Research Board OF Canada

Volume 31, No. 5, May 1974

Limnology in Canada — *Special issue prepared for the XIX Congress, International Association of Limnology (SIL)*

Environment Canada
Environnement Canada
Fisheries and Marine Service
Service des pêches et des sciences de la mer

Journal
Fisheries
Research
Board
Canada

Volume 31, No. 5, May 1974

This number was issued on May 31, 1974.

Environment Canada
Fisheries and Marine Service

Environnement Canada
Service des pêches et des sciences de la mer

The *Journal of the Fisheries Research Board of Canada* has been published continuously since 1901, previously as *Contributions to Canadian Biology* 1901–1925, *Contributions to Canadian Biology and Fisheries*, 1926–1934, and *Journal of the Biological Board of Canada*, 1934–1937. The *Journal* is published in annual volumes of twelve numbers.

The *Journal* is devoted to original research papers and notes concerning aquatic organisms or environments relevant to Canada. Review articles that are critical appraisals of broad areas of research are also welcomed. Submissions in English or French are accepted without limitations as to origin, but must not have been published or copyrighted. Details on submissions are given in the guides to authors and typists at the back of this issue. Reprints of the guides are available free from the Office of the Editor.

A charge of $30.00 per page is made for articles published. When submitting a manuscript, an author should state that his institution will accept this charge.

Subscription rates to the *Journal* are: Canada, $15.00 per year; other countries, $18.00. Single issues are $1.50 and $1.75, respectively. Orders must be sent directly to Information Canada, Ottawa, Canada, K1A 0S9.

Le *Journal of the Fisheries Research Board of Canada* a été publié sans interruption depuis 1901, sous les noms suivants: *Contributions to Canadian Biology* de 1901 à 1925, *Contributions to Canadian Biology and Fisheries* de 1926 à 1934, *Journal of the Biological Board of Canada* de 1934 à 1937 et finalement le nom qu'il porte présentement. Le *Journal* paraît annuellement en un volume comprenant douze numéros.

Le *Journal* est consacré aux études sur des recherches originales et aux notes concernant les organismes et les environnements aquatiques pertinents au Canada. Des critiques concernant des ouvrages généraux sont aussi appréciés. Des soumissions en anglais ou en français sont acceptées sans limitations d'origine, sauf si elles ont déjà été publiées ou déposées. Les manuscrits soumis pour publication doivent être préparés suivant les directives publiées dans ce numéro sous les rubriques "Guide des auteurs" et "Guide pour secrétaires d'auteurs." On pourra se procurer gratuitement une copie de ces directives en s'adressant au bureau du Directeur de la publication.

Les frais sont de $30.00 par page pour la publication des articles. Quand un auteur soumet un manuscrit, il doit spécifier que son institution accepte les frais.

Les frais de souscription au *Journal* sont: au Canada, $15.00 par année; autres pays, $18.00. Une seule copie se vend $1.50 et $1.75 respectivement. Les commandes doivent être envoyées directement à Information Canada, Ottawa, Canada K1A 0S9.

Editor and/Rédacteur et *Director of Scientific Information* *Directeur de l'information scientifique*	J. C. STEVENSON, PH.D.
Deputy Editor *Sous-rédacteur*	J. WATSON, PH.D.
Associate Editor *Rédacteur associé*	L. W. BILLINGSLEY, PH.D.
Assistant Editor *Rédacteur adjoint*	R. H. WIGMORE, M.SC.
Production/Documentation	J. CAMP G. J. NEVILLE/PAULA IRVING
French Abstracts/Résumés francais	Y. JEAN, PH.D.

Bureau du directeur de la publication
Service des pêches et des sciences de la mer
Ministère de l'Environnement
116, rue Lisgar, Ottawa, Canada
K1A 0H3

Office of the Editor
Fisheries and Marine Service
Department of the Environment
116 Lisgar Street, Ottawa, Canada
K1A 0H3

Volume 31, No. 5, May 1974

Journal
OF THE Fisheries
Research
Board
OF Canada

EDITOR'S FOREWORD

Canada has more lakes than any country in the world, and hence it is fitting that Canada will host the 19th triennial congress of the Societas Internationalis Limnologiae (International Association of Limnology) in August 1974 in Winnipeg, situated near the center of Canada's innumerable lakes.

Prior to each congress it has been customary for the sponsoring country to publish a report on its progress in limnological research. Two years ago, Dr J. R. Vallentyne, the national chairman of this congress, selected the *Journal of the Fisheries Research Board of Canada* as the publishing agency. Drs Harold H. Harvey and Glen H. Geen sought contributors who would reflect the present state of limnological research in Canada, and kindly acted as special editors of this volume.

The *Journal* is privileged to devote its May 1974 issue to this special collection of papers on Canadian limnology.

J. C. Stevenson
Editor and Director of Scientific Information

Printed in Canada (J3341)

Préface
du
Directeur de la Publication

Il y a plus de lacs au Canada que dans tout autre pays du monde. Il sied donc que le Canada soit l'hôte du dix-neuvième congrès triennal de la *Societas internationalis limnologiae*, l'Association internationale de limnologie, en août 1974, dans la ville de Winnipeg, au coeur même d'une contrée très riche en lacs.

Avant chaque congrès, l'usage veut que le pays hôte publie un rapport sur ses réalisations en recherche limnologique. Il y a deux ans, le Dr J. R. Vallentyne, président national du congrès de 1974, a choisie le *Journal* de l'Office de recherches sur les pêcheries comme organe de diffusion de ce rapport. Le Dr Harold H. Harvey et le Dr Glen H. Geen se sont mis en quête d'auteurs qui représenteraient bien l'état de la recherche dans le domaine limnologique au Canada. Eux-mêmes ont eu la générosité d'assumer la tâche de compilation et de revision du présent volume.

C'est donc un honneur pour la direction du *Journal* d'offrir au lecteur ce numéro de mai 1974, entièrement consacré aux textes traitant de la limnologie au Canada.

J. C. Stevenson

Rédacteur et Directeur de l'information scientifique

Introduction to Limnology in Canada[1]

Harold H. Harvey

Department of Zoology, University of Toronto, Toronto, Ont. M5S 1A1

and Glen H. Geen

Department of Biology, Simon Fraser University, Burnaby, B.C. V5A 1S6

This special issue of the *Journal of the Fisheries Research Board of Canada* has been prepared to mark the occasion of the Assembly of the XIX Congress of the International Association of Limnology in Winnipeg, August 1974. It was prompted by the realization that limnology in Canada has changed greatly since the reviews prepared for the book *Limnology of North America* which was published following the XV Congress in Madison, Wisconsin. The members of the XIX Limnological Congress Organizing Committee felt that a commemorative volume would serve as a valuable updating and provide Congress participants and others with an overview of the present major thrusts in Canadian limnology.

The origins of limnological work in Canada are linked strongly to fish and fisheries problems. This is suggested by the titles of the principal outlets that have existed over the years for publication of the results of aquatic research in Canada. *Contributions to Canadian Biology* began in 1902 as studies from the Marine Biological Station of Canada. In 1926 this journal was expanded to *Contributions to Canadian Biology and Fisheries*, and published studies from the various biological stations operated under the direction of the Biological Board of Canada. In 1934 the series was changed in name to *The Journal of the Biological Board of Canada*. In 1937 the Biological Board was reconstituted as the Fisheries Research Board of Canada and the name of the *Journal* changed accordingly. This journal has provided a stimulus for research and excellence in research in the aquatic sciences generally and fish and fisheries in particular. A review of these publications and the *Proceedings of the International Association of Theoretical and Applied Limnology* points out that this emphasis on the study of fish populations has resulted in a closer integration of limnology and fisheries in Canada than is common elsewhere.

The formative period of limnology in Canada was the years 1920–50. Much of the work of this time consisted of the essential description of physical and chemical features of lakes, plus assessment of species composition, seasonal abundance, and distribution and growth of organisms in these waters, particularly as related to fish and problems of fish production. Almost all of this research was on the lacustrine environment, with little attention paid to lotic systems despite the abundance of streams and rivers in Canada. During these early years, much of the initiative and funding for research came from the individual governments of the provinces.

In Ontario, for example, research was conducted on Lake Nipigon up to 1926, on Lake Nipissing commencing in 1929, and at Opeongo Lake from 1936 to the present. Professor J. R. Dymond and W. J. K. Harkness played a major role in expanding provincial involvement in limnological research. Professor F. E. J. Fry was instrumental in the establishment of research stations at Maple and South Bay (Lake Huron), and continued the center of learning in fish ecology and physiology at the University of Toronto. The Province of Ontario continued to expand its research effort, and there are now research stations on four of the Great Lakes, plus fishery management units on seven other large lakes. In 1967 the Lake Inventory Program was organized; since that time lakes in Ontario have been surveyed at the rate of about 1000 per year. To this has been added a stream inventory, commencing in 1972, with a capacity to study some 400 km of rivers and streams annually.

The history of limnology in Quebec was reviewed in detail by V. Legendre (Fry and Legendre 1963). Since that time some considerable reorganization has occurred in that province. A large limnology laboratory, "Centre québécois des sciences de l'eau" of the Institut national de la recherche scientifique, was constructed on the campus of the Université du Québec, Québec. The terms of reference of this organization are to conduct basic and applied research in various disciplines of conserva-

---

[1] This paper, part of a special issue that comprises a comprehensive review of Limnology in Canada, was prepared to mark the 19th Congress of the International Association of Limnology (SIL), in Winnipeg, Man., during August 1974.

Printed in Canada (J3330)

tion and management of water resources. Current major projects include: 1) Development of methods for evaluation of water resources, including identification of important characteristics. 2) Establishment of methods for synthesis and modelling of watersheds. 3) Development and evaluation of criteria for the management and exploitation of water for human consumption. 4) Development of the methodology for maintenance of water quality on a regional basis. In addition, the various departments within the provincial governments have maintained their historic responsibilities. Thus the Service de la faune du Québec of the Ministère du Tourisme, Chasse et Pêche conducts limnological research insofar as it affects the fish and game. The Service du qualités des eaux of the Ministère des Richesses Naturelles has responsibility for research in limnology as it relates to water quality.

In the Atlantic provinces much of the early limnological research was directed at streams and rivers, with a view to increasing production of Atlantic salmon (*Salmo salar*). A. G. Huntsman of the Atlantic Biological Station was an active contributor in this field for half a century. During the 1940s through to the 1960s F. R. Hayes of Dalhousie University studied several aspects of limnology on lakes in the Maritime Provinces, including water chemistry, bottom sediments, and fish production. M. W. Smith of the Atlantic Biological Station investigated a variety of approaches to the enrichment and hence increased productivity of nutrient-poor and dystrophic lakes. The quality of streams and rivers, especially as it affects young and adult Atlantic salmon, continues to be a major limnological concern in the Maritime Provinces.

In Manitoba there was a brief period of research on Lake Winnipeg during the 1930s, with notable contributions by F. Neave and A. Bajkov. Thereafter, research lagged until a station of the Fisheries Research Board of Canada was located in Winnipeg (1945–58), and the province increased its program of fisheries research and lake surveys. Currently, provincial limnological research is being directed at problems of immediate importance: the eutrophication of Lake Winnipeg, the effect of pulp waste in the Saskatchewan River, and the entry of mining effluent into northern lakes and rivers. Based on 12 yr of monitoring the southern basin, Lake Winnipeg has been changing at a rate approximately one-tenth that of Lake Erie, a gain of 10 ppm TDS in 39 yr. New impetus will be added to limnological research in north–central Manitoba with the opening of the Grand Rapids Fisheries Station, a combined hatchery and research facility, in 1974.

Intensive surveys of large Saskatchewan lakes were commenced by D. S. Rawson, and during the past 20 yr the 200 largest lakes have been studied. Current provincial research in limnology now has two main directions: assessment of environmental change, such as that brought about by the petrochemical industry on the Saskatchewan River; secondly, management of fish populations in large lakes, based on the historic criteria of Rawson — morphoedaphic features, commercial catch of fish, and fish samples from standard gangs of gillnets.

From its origins in Rawson's studies of alpine lakes in the 1930s and 1940s, and R. C. Miller's work on lakes and streams in the 1940s and 1950s, limnology sponsored by the Province of Alberta has evolved in two directions. Routine lake surveys have been continued primarily for purposes of fisheries management. In addition, recent emphasis has been on the effect of industrial development in specific areas, e.g. the impact of thermal effluents on Wabamun Lake.

In British Columbia the limnological work of R. E. Foerster and W. E. Ricker during the 1930s was based at the Pacific Biological Station of the federal government. In the 1950s and 1960s W. A. Clemens and P. A. Larkin developed a strong school in aquatic studies at the University of British Columbia. At this time an extensive program of lake surveys was launched by the province, some of the results of which have been reported by Northcote and Larkin (1956). Considerable data on B.C. lakes, especially as it relates to salmon production, has been collected by the International Pacific Salmon Fisheries Commission and the federal government, through the Pacific Biological Station. Current provincial limnological research is problem-oriented, with emphasis on the effects of hydroelectric development and changing water quality.

The results of the wide array of major studies collated in this volume indicates there has been a profound shift in limnology in Canada in recent years. This is especially apparent if a comparison is made between this volume and the five papers that dealt with limnology in Canada (Northcote and Larkin; Fry and Legendre; Smith; Livingstone; Beeton and Chandler) and that were included in *Limnology in North America* in 1963. These changes in Canadian limnology may be summarized as:

1) Greatly increased federal government involvement, as expressed in the construction and staffing of the Canada Centre for Inland Waters at Burlington, Ontario, and the Freshwater Institute at Winnipeg, Manitoba.

2) The support of the National Research Council of Canada for Canadian participation in the International Biological Program. The limnological component of this comprised detailed studies of two lakes, Marion Lake in southern British Columbia and Char Lake in the high arctic.

3) The launching of large, federally supported studies on water quality and eutrophication, such as those in the Experimental Lakes Area in northwestern Ontario and the massive research program on the Great Lakes. Considerable effort has also been devoted to integrating limnological work into decision-making regarding future uses of waters. The Okanagan Basin Lakes and the St. John River Basin studies are notable examples.

4) Major studies arising out of developments, either existing or proposed, in the arctic and subarctic. These include the proposed Mackenzie Valley pipeline, the diversion of the Churchill River to the Nelson River, and associated damming of both systems, and the James Bay development.

5) An increase in government-sponsored studies on arctic and subarctic lakes and rivers as part of a program to describe the life histories and population dynamics of economically important fish species in these areas.

6) Increased support from federal government research and management agencies for aquatic research at the universities, formerly by the Fisheries Research Board of Canada, and now by the Department of the Environment.

7) Major increases in provincial activity, particularly in Ontario, which has launched the Lake and Stream Inventory Programs. Increases in provincial support for research, as in the construction and operation of the field station at West Blue Lake, Manitoba, are becoming more frequent.

8) Greater attempts have been made at synthesizing information, both local and international, as in the Symposium on Salmon and Trout in Streams (Northcote 1969) and the SCOL Symposium in August 1971 (Loftus and Regier 1972), and the Technical Conference on Fishery Management and Development, 1973.

9) Student interest in limnology has increased greatly and more universities are offering courses and programs in this area.

10) The number of practising limnologists in Canada has increased greatly. Membership in SIL has increased from approximately 63 in 1964 to almost 200 in 1974. Participation in allied organizations in Canada has increased similarly. For example, registration for the annual meeting of the Canadian Committee on Freshwater Fisheries Research (CCFFR) has trebled in the last decade and now exceeds 300.

11) Some aspects of limnology have changed considerably, due in part to advances in computing technology. More attempts are being made to study and model lakes as whole systems, as opposed to investigating some aspects of a lake.

12) There has been a marked increase in the number of private companies engaged in aquatic studies. Their work is mainly related to assessment of probable or actual effects of industrial development on aquatic systems.

These changes are most apparent in the more heavily populated areas of Canada, particularly in Ontario and southern British Columbia. In other parts of the country, many necessary studies describing lakes and streams and their populations are underway to provide the background information on which to base future management recommendations, or to assess the effects of proposed industrial development. This is particularly evident in the Prairie Provinces and east from Quebec.

The diversity in the state of limnology in Canada is reflected in the contributions to this issue of the *Journal*, which were selected on a regional basis with particular attention to the size and scope of the work. Although we solicited a number of review papers, preference was given to research projects which were too long to be presented to the Congress in the usual way and too large to be included in the Proceedings. Obviously the preparation of publications such as this cannot coincide with the completion of every major study in the country. Many had to be omitted for this reason including those on Memphremagog Lake, the Mackenzie Delta, Great Central Lake, splake plantings in Ontario, the Ottawa River study, the James Bay Project, and so forth. However, we believe that the papers presented in this issue are representative of the major trends and will provide the basis for understanding the state of the science of limnology in Canada at this time.

BEETON, A. M., AND D. C. CHANDLER. 1963. The St. Lawrence Great Lakes, p. 535–558. *In* D. G. Frey [ed.] Limnology in North America. Univ. Wisconsin Press, Madison, Wis.

FREY, D. G. [ed.] 1967. Limnology in North America. Univ. Wisconsin Press, Madison, Wis. 734 p.

FRY, F. E. J., AND V. LEGENDRE. 1963. Ontario and Quebec, p. 487–519. *In* D. G. Frey [ed.] Limnology in North America. Univ. Wisconsin Press, Madison, Wis.

LIVINGSTONE, D. A. 1963. Alaska, Yukon, Northwest Territories and Greenland, p. 559–574. *In* D. G. Frey [ed.] Limnology in North America. Univ. Wisconsin Press, Madison, Wis.

LOFTUS, K. H., AND H. REGIER [ed.] 1972. International Symp. on Salmonid Communities in Oligotrophic Lakes. J. Fish. Res. Board Can. 29: 611–986.

NORTHCOTE, T. G. [ed.] 1969. Symp. on Salmon and Trout in Streams. H. R. MacMillan Lecture in Fisheries, Univ. British Columbia, B.C. 388 p.

NORTHCOTE, T. G., AND P. A. LARKIN. 1956. Indices of productivity in British Columbia lakes. J. Fish. Res. Board Can. 13: 515–540.

1963. Western Canada, p. 451–485. *In* D. G. Frey [ed.] Limnology in North America. Univ. Wisconsin Press, Madison, Wis.

SMITH, M. W. 1963. The Atlantic provinces of Canada, p. 521–534. *In* D. G. Frey [ed.] Limnology in North America. University of Wisconsin Press, Madison, Wis.

Lakes — The Vital Water Resource in Canada[1]

J. P. BRUCE

Department of the Environment, Environmental Management Service
Canada Centre for Inland Waters, Burlington, Ont. L7R 4A6

THERE are myths about most countries of the world. One of the myths about Canada is that there is an almost unlimited water resource to use and abuse. Most myths, when examined carefully, have an element of truth, as does this idea about Canada's waters. But this myth is misleading in many ways. For each square mile of land area, Canada's river flows are close to the world average. Canadian rivers discharge about 91,000 m^3/s (3.2 million ft^3/s), or about 9% of the world's river discharge to the oceans. Canada has well below average endowments of groundwater, which is the major freshwater source in most countries. Much of the land is permanently frozen or has a granitic base inhospitable to groundwater aquifers of significant volume.

The truth of the myth lies in Canada's lakes. Lakes are part of, indeed they essentially form, the landscape from Newfoundland to British Columbia. Even in the most populous province, Ontario, there are said to be 250,000 lakes, many of which have not even been named. In addition to myriad small and medium-sized lakes which dot the landscape, Canada has within its boundaries, or shares with the USA, 8 of the 22 largest lakes of the world. As if that weren't enough, Canada has created 12 of the world's largest man-made lakes — greater than 100,000 acre-feet ($1.23 \times 10^9 m^3$) of storage, for power production, irrigation, and other purposes.

It is hardly surprising then that a major focus of water research in Canada has been on limnology, and that a major emphasis in water management programs has been directed towards optimum use of lake waters, both as a resource and as an aquatic environment.

Intensification of limnological research in Canada in the past decade has come about largely because of the dawning realization in government and by the public that use of lakes for one purpose may eventually seriously interfere with other uses. Where the lake waters are free to anyone, excessive and preemptive uses will have serious and long-term consequences that could gradually turn our lakes into liabilities rather than resources for future generations.

What are some of these uses of lake waters across Canada?

Use of Lake Waters

RESIDENTIAL AND INDUSTRIAL

Many municipalities, including some of our largest ones, draw water supplies for residential and industrial uses from lake systems. Practically all withdrawals from rivers are strongly affected in quantity and quality by upstream lakes or reservoirs. Total municipal (residential, commercial, and public) and rural residential withdrawals in 1970 were about 1.8 billion gallons/day (8.1 billion liters/day). Of residential usage, which is about one-half of the municipal withdrawals, about 38% is used for toilet-flushing, 26% for bathing and personal use, 17% for washing of various sorts, 15% for lawn watering and other outdoor uses, and only 4% for drinking and cooking. Water withdrawals by primary industries were about 6.3 billion gallons/day (28.4 billion liters/day) in 1970, 53% of the withdrawals being from the Great Lakes–St. Lawrence system. Two industries — pulp and paper, and metal smelting and refining — account for two-thirds of water uses in manufacturing, and most of the balance is used by chemical, petroleum, food, and plastics industries. These industries and the residences (municipalities) return the water drastically altered; this used water, if not treated or purified, constitutes a major source of lake pollution.

AGRICULTURAL

Irrigation water withdrawals are concentrated in the Prairie Provinces. Three-quarters of the annual 1.7 million acre-feet ($2.1 \times 10^9 m^3$) of irrigation water usage is in Alberta, Saskatchewan, and Manitoba; nearly all the rest is in interior British Columbia, where it is used for fruit growing (Lake Okanagan watershed), and in the Fraser Valley. Some 40% is consumed and does not return to the water courses or lakes. Stock watering with-

---

[1] This paper, part of a special issue that comprises a comprehensive review of Limnology in Canada, was prepared to mark the 19th Congress of the International Association of Limnology (SIL), in Winnipeg, Man., during August 1974.

Printed in Canada (J3261)

drawals are about 300 million gallons/day (1.3 billion liters/day) and are more evenly spread across Canada. These agricultural water uses have a significant impact on water resources, both in quantity (much of the irrigation water is evaporated) and quality. Waters returned to lakes and rivers are rich in nutrients, salts, and toxic substances. In addition, changes in the quality and quantity of runoff are caused by land cultivation and changing land use patterns in suburban areas.

ELECTRICITY PRODUCTION

Water is essential to production of electrical energy; it provides potential energy for hydro power plants, and is the main coolant in thermal power-generating stations. Slightly more than 200 billion kilowatt hours (3.6 MJ) of electricity was produced in Canada in 1970. Of that total, 77% was generated at hydroelectric plants and the remainder at thermal plants fired by coal, oil, or nuclear fuels. About 65% of the water used in electrical power generation in Canada was in the Great Lakes–St. Lawrence Basin. Reservoirs and dams for hydroelectric power may have significant environmental effects on downstream rivers and lakes and, of course, within the area flooded by the reservoirs themselves. They can also have potentially serious effects on native populations dependent on fishing and hunting as in the James Bay area, northern Manitoba, and the Peace River Delta. The by-products of thermal power generation are large amounts of waste heat and, in the case of nuclear plants, small amounts of radioisotopes, which are discharged to lake systems. Effects of such discharges on the aquatic environment are just beginning to be understood.

WATER TRAFFIC

Navigation by both commercial and pleasure craft is a major use of Canada's inland lakes and waterways. The Great Lakes–St. Lawrence Seaway system dominates, in terms of tonnage shipped and value of navigation activities. Fifty-three million tons of cargo were transported in the Montreal–Lake Ontario section of the Seaway in 1971. Major cargoes are iron ore upbound, and overseas grain shipments downbound from the Lake Superior ports in the heart of the continent. Log driving by river and transportation over lakes is still important to the pulp and paper industry, especially in Quebec. An increasing traffic in shipment of chemicals from overseas ports into the Great Lakes and out of large chemical industry complexes in Great Lakes cities has caused concern over protection of water against accidental spills. Besides the danger of chemical and oil spills there is the threat of pollution from human and other wastes from vessels, not only in the Great Lakes system, but in "resort" lakes throughout the country. In the Great Lakes, regulation of wastes from ocean-going vessels is a particularly difficult and important problem, as the Lakes constitute one of the few water highways in the world also used for drinking water for some 30 million people.

FISH AND WILDLIFE

The value of fish and wildlife resources is only partly understood in terms of catch statistics and economic measures. The well-being of sensitive fish species and other pollution-sensitive creatures has come to provide important indicators of the health of lake systems. Commercial fishing and the fur trade are of major historical importance in the Canadian economy and remain a primary source of income in some parts of the country. About 9% of the Canadian commercial fisheries income of $178 million (1969) is from the lakes, mostly the Great Lakes and the major lakes of Manitoba and the Northwest Territories. About 40,000 full-time trappers, mostly native peoples, still earn their living from the water-dependent furbearing animals of northern and central Canada, with a total income estimated at $18 million (Pimlott et al. 1971).

RECREATION

Water-based recreation creates one of the most socially important and rapidly growing demands for uses of lakes and waterways. Indeed, even in southern Ontario, adjacent to the Great Lakes, a number of small man-made lakes have been created for recreational purposes near large urban centers to meet the demand for water-based recreational facilities. Although recreation needs are difficult to quantify, a 1969 survey (Anon. 1971) states that 44% of Canadians participate in swimming (from 36% in the Atlantic Provinces to 53% in Ontario), and 29% in boating activities. An estimated 3.2 million anglers fish Canada's waters annually, spending about $600 million on goods and services related to sports fishing. The rapid growth of the tourist industry and the resulting demand for water-based recreation is providing new and powerful incentives to preserve lakes in a "nonpolluted" condition. However, recreational water uses in themselves also create water quality problems, and pollution of recreational lakes now frequently occurs because of inadequate sewage treatment at cottages and untreated discharges from pleasure craft.

Water Use Conflicts

These many uses of lakes and rivers result in obvious conflicts. Waters used to carry away wastes are often unfit for recreation; irrigation water withdrawals may affect boating uses of lakes by lowering levels; and so on.

Optimum resolution of such conflicts requires an extensive and intensive understanding of lake and river systems and their behavior. What are some of the major lake problems brought about by the outlined patterns of use and what is being done about these problems in Canada? A long list would include such social–political problems as shore-property ownership and public access to lakes, such geological and land-use problems as shore erosion and flood damage to land and buildings, and such hydrological problems as improved control or at least forecasting of lake level fluctuations on the lakes most intensively used. However, to permit analysis in some depth, this discussion will deal only with three aspects of lake water quality — occurrence of toxic substances, discharge of waste heat, and acceleration of cultural eutrophication.

TOXIC CONTAMINANTS

Toxic materials of many types now enter the lake environment. To date, no major effects on human health from toxic-chemical contamination of waters has been reported in Canada. However, mercury and PCB (polychlorinated biphenyls) concentrations in some lake sediments and lake biota are high enough to warrant the control programs instituted for these substances and to require the careful monitoring of lakes, fish, and foods which is now underway. Much loading to lakes occurs through discharges from industries.

For lakes more remote from heavily industrialized areas, transport of toxic substances through the atmosphere and into lakes is being recognized as a major source of such contaminants. Even to Lake Ontario, subject to large waste discharges from primary and secondary industries, especially through the Niagara River, atmospheric sources are estimated to contribute between 15 and 36% of the Niagara River lead input to the Lake and 58–85% of the zinc loading (Shiomi and Kuntz 1973). In Lake Superior, with a relatively undeveloped shoreline, much higher concentrations of Cd, Cu, Fe, Ni, Zn, and Pb are found in precipitation than in lake waters, and current studies will undoubtedly show atmospheric sources of such metals to be a dominant or at least highly significant proportion of total inputs. A further load of toxic substances, especially pesticides, enters our lakes from land drainage sources or from return flows in irrigated basins.

Effects of some toxic substances such as mercury and DDT on aquatic ecosystems and human health have been of major public concern. In addition to long-term effects which are difficult to assess, toxic substances have created serious disruptions of commercial fishing, dredging operations, and angling. To be better-armed technically to respond to future governmental and public concerns over toxic substances, biologists and chemists at the Canada Centre for Inland Waters identified some 20 substances likely to be of future concern, in a rough order of priority. As a first step, economic geographers were asked to determine the extent of importation, mining or manufacturing, and use in industry of these substances, mostly metals and organochlorides. For example one of these toxic substances, cadmium, is consumed and produced in Ontario at an annual rate of about 2,351,300 lb (1,052,000 kg) (1970 estimates, B. Lymburner and H. Knoll, Canada Centre for Inland Waters, Burlington, Ontario, unpublished data). This contributes to a continuous buildup of the stock of industrial products containing cadmium. Actual cadmium loadings entering the Great Lakes are directly proportional, through attrition, to the localized production and consumption level of this stock. From surveys of the 20 substances, including cadmium, Environment Canada has assessed which of these possible problem materials are most likely to be entering lakes and rivers in significant quantities and where the highest concentrations are likely to be. This has permitted design of biochemical research programs concentrating on pathways and effects of the most critical substances. It has also permitted design of water and sediment sampling networks to monitor in a more selective way trends in concentrations of these substances.

However, the ways in which toxic substances, such as cadmium and PCB's, are diffused from sewers and other sources into lakes, deposited in sediments, and cycled through the food chain, are not completely known or understood, even when the toxicology of the substances is well known. Many important microbiological, chemical, and physical processes involving toxic materials occur in surface layers of sediments, and we are only beginning to understand how some of these processes work in lakes.

WASTE HEAT DISCHARGES

A second problem in lake management, that of waste heat discharges, has not yet caused serious problems in Canada except in a few locations; but it promises to present difficult water-use conflicts within the next few decades. For example, in the Laurentian Great Lakes the present (1968) discharges of waste heat amounting to 10 × 10^{10} BTU/hour (2.5 × 10^{10} kcal/hour) are expected to increase 11-fold by the year 2000 (Denison and Elder 1970). Heated discharges from domestic sewage and steel plants represented a significant portion of the heat added by man's activities along some parts of the Great Lakes shoreline in 1968. However, by 2000 AD the overwhelmingly dominant source is likely to be from fossil- and nuclear-fuelled electric power generating stations. In fossil-fuel plants, about 37% of the energy produced is in the form of power, 50% is heat loss to water, and the remainder (13%) is heat discharged to the atmosphere. In the Candu-type nuclear reactor only 29% of the energy produced is electrical power; about 70% is waste heat discharged to the waters. (H. A. Clarke unpublished data).

In Canada, most major economical hydroelectric power sites have been used or are presently being exploited. Thermal discharges are already of concern in several lakes, such as Lake Wabumun near Edmonton, Alta., and Wascana Lake at Regina, Sask. To meet increasing power demands, thermal-power generation will increase dramatically. In the next three decades a 25-fold increase in cooling water requirements is projected outside of the Great Lakes Basin (Montreal Engineering Co. Ltd. 1971). Some of this demand will be met by coastal waters in British Columbia and the Atlantic Provinces, but in most of Canada waste heat will be discharged to lakes and rivers. Freshwater evaporation losses due to this increased water use many reach 850 million gallons/day (3.8 billion liters/day), not including losses from the Great Lakes.

Much work has been done on the probable effects of heated plumes on the aquatic environment. Many effects, both harmful and beneficial, have been documented in the literature; they nearly always seem to involve significant changes in production and shifts in distribution of aquatic organism species. However, present knowledge does not permit accurate prediction of effects of major heated discharges, either individually or collectively. Thus development of suitable regulations and controls which may be required to protect lakes and rivers is seriously inhibited.

CULTURAL EUTROPHICATION

The third example of how conflicts in uses of lake waters arise is the process of cultural eutrophication, wherein man's use of lakes as a receptacle for nutrient-laden municipal wastes and drainage from agricultural and urban lands has resulted in over-enrichment of many lakes. Sometimes enrichment has had beneficial effects; more fish may thrive for many years before major hypolimnetic oxygen depletion begins and algal growths foul water intakes, beaches, and boating and swimming areas to a serious extent. But nutrient-control programs to slow cultural eutrophication are essential to multipurpose use of many of our lakes.

Limnologists have learned a great deal about eutrophication of lakes, but it is only in the past few years that models relating the trophic state of lakes to nutrient loads have been developed and have permited initial quantitative management decisions. An important synthesis of available data on the world's lakes, in a form applicable to management, has been made by Vollenweider (1968). He initially produced graphs relating trophic states to total nitrogen and phosphorus loadings per unit surface area and mean depth of the lakes. Recently he introduced the flushing time of the lake system as another important factor.

Such relations clearly give water managers a method of estimating reductions in nutrient loading needed to achieve mesotrophic or oligotrophic conditions in a given lake, provided the nutrient inputs to the lake system are reasonably well known. Vollenweider's work was a major influence on recommendations for phosphate control programs resulting from studies conducted for the International Joint Commission (IJC) on Pollution of lakes Erie and Ontario, and the International Section of the St. Lawrence River (Anon. 1970). This report, in turn, formed the basis for the subsequent Canada–U.S. Agreement on Great Lakes Water Quality signed by President Nixon and Prime Minister Trudeau in April 1972 (Anon. 1972).

A particularly interesting example of rapid application of limnological research results to a management program is the eutrophication control program for Lake Erie. Phosphate control programs for reversal of accelerating eutrophication, incorporated in the Canada–U.S. Agreement, were based in part on the IJC report and Vollenweider's graphs, but were also strongly influenced by a major study (Project Hypo) of Lake Erie in 1970–71. In early autumn of 1970, anoxic conditions in the hypolimnion of the central basin of the lake, as measured during Project Hypo, extended over an area exceeding 6000 km^2 (Burns and Ross 1972). Scientists demonstrated that 88% of oxygen uptake was due to bacterial degradation of algae which sank to the bottom during summer and early fall. Phosphates returned from the sediments to the water under these anoxic conditions 11 times faster than when oxygen was present in bottom waters. By making a phosphate budget, calculating both internal and external loadings, Burns and

Ross concluded that "The Central Basin is now changing from being a settlement basin for phosphorus to a production basin during the summer stratification period. Phosphorus input to Lake Erie must be reduced immediately; if this is done, a quick improvement in the condition of the lake can be expected; if it is not done, the rate of deterioration of the lake will be much greater than it has been in recent years."

But how much reduction would be necessary to reach the point where anoxic conditions no longer occur? Dobson and Gilbertson (1971) reviewed available historical records of depletion rates of oxygen in the central basin hypolimnion from time of late spring stratification to breakdown of the thermocline in early fall. Sufficient data to assess trends had been obtained by the University of Ohio in the early 1930s, the Great Lakes Institute of the University of Toronto in the late 1950s and early 1960s, and by the Canada Centre for Inland Waters in recent years. Depletion rates generally increased from 1930 to 1970, with rate of increase appearing to be much greater in recent years. The critical year was 1960, when the rate of hypolimnetic oxygen depletion began to consistently produce anoxic conditions by early fall in the central basin. Gilbertson et al. 1972 then compared historical oxygen depletion rates with estimates of historical phosphorus loadings, and a remarkable linear relationship resulted (Bruce 1973). From this an estimate was made of phosphorus reductions needed to achieve pre-1960 conditions. In the Canada–U.S. Agreement, phosphorus control programs were designed to achieve such reductions in external phosphorus loading to Lake Erie by the end of 1973. Table 1 is taken from the Agreement and indicates the agreed loading reductions. The date (1973) for achieving most of the phosphorus control objectives is earlier than originally recommended by IJC (1975) and was agreed to by the federal governments, states, and provinces because of the Project Hypo findings.

This study provided a short-term specific objective for "restoration of year-round aerobic conditions in the bottom waters of the central basin of Lake Erie" in addition to the general, long-term objectives for trophic state provided by the Vollenweider model. The relationship used in this case are, of course, mainly empirical. However, they make the most of the data and of our present understanding of limnological processes, and put them in a form usable by water managers and pollution control agencies.

Control of phosphorus loadings to Erie and Ontario as outlined in the International Agreement is to be achieved by a combination of detergent reformulation and removal by chemical precipitation of phosphorus at municipal and industrial wastewater treatment facilities. All Great Lakes municipal treatment plants with discharges greater than 1 million gallons/day (4.5×10^9 liters/day) are expected to achieve a maximum of 1 mg/liter phosphorus in their effluent by the end of 1973 for Lake Erie, and 1975 for Lake Ontario.

TABLE 1. Estimated annual phosphorus loadings and reductions in loadings, in short tons per year, to Lake Erie (including Lake St. Clair and the St. Clair and Detroit rivers).

	1971	1972	1973	1974	1975	1976
U.S.						
Baseload	25,800	26,400	27,000	27,600	28,300	28,800
Reduction	100	5,200	9,800	15,100	16,000	17,300
Residual load	25,700	21,200	17,200	12,500	12,300	11,500
Canada						
Baseload	3,300	3,300	3,400	3,500	3,500	3,600
Reduction	100	100	600	1,400	1,400	1,400
Residual load	3,200	3,200	2,800	2,100	2,100	2,200
Input from Lake Huron	2,300	2,300	2,300	2,400	2,400	2,400
Totals						
Baseload	31,400	32,000	32,700	33,500	34,200	34,800
Reduction	200	5,300	10,400	16,500	17,400	18,700
Residual load	31,200	26,700	22,300	17,000	16,800	16,000

Phosphorus reduction programs for control of cultural eutrophication are initiated or under development in many other locations in Canada. These programs include regulated reduction in phosphates in detergents, and, for those lakes where additional reductions in phosphate loadings are required and possible, introduction of chemical precipitation of phosphates at sewage treatment facilities (Prince and Bruce 1972). Such facilities have been built or are being planned for Okanagan Lake, B.C., and the Qu'Appelle Lakes, Sask., as well as for the lower Great Lakes.

Nutrient Control

But regulation of natural and social systems is never as simple as it appears. So it is with phosphate control. Chemical precipitation at sewage treatment plants generates a much increased volume of chemically enriched sludge which must be handled and disposed of. Disposal on agricultural land is an attractive possibility but do we yet know enough about optimum application rates, toxic metal uptake by plants, and virus survival in sludges? Detergent reformulation also has its problems; these will be examined more extensively.

PHOSPHATE REGULATIONS

The first recommendation of the IJC in 1970 for control of nutrients was to "reduce and eventually eliminate phosphates in detergents." The federal and provincial governments agreed, after a study of the Board's recommendations and of eutrophication problems and potential problems throughout Canada, that the federal government should introduce legislation to control use of "nutrients in cleaning products."

The Canada Water Act, incorporating the clause permitting regulation of nutrients in cleaning products, passed the Commons and Senate in the early summer of 1970, and the first regulations under the nutrient control clause became effective August 1, 1970. The detergent industry had been informed in January 1970 of the government's intention, concerning regulations under the Act, to limit the amount of phosphates in laundry detergents to a maximum of 20% expressed as phosphorus pentoxide (P_2O_5). Most detergent powders had contained from 16 to 38% P_2O_5. This initial limitation reduced the amount of detergent phosphates entering Canadian lakes and rivers by 25–30%.

The August 1970 regulation limiting detergent phosphates was announced as the initial step in this part of the phosphate control program. It was assumed that the 20% P_2O_5 limit could be met with minor adjustments in formulation, as many detergents already had less phosphates. However, further reductions or total elimination of phosphates would require major reformulation, with large-scale introduction of alternative substances.

A number of possible replacements for STPP (sodium tripolyphosphate) have been seriously considered and used. These include carbonate/silicate, borate, citrate, soap plus dispersant, other synthetic organics, and NTA (nitrilotriacetic acid, trisodium salt monohydrate); but only carbonate/silicate, citrate, and NTA are serious contenders at present.

CARBONATE/SILICATE

Carbonate/silicate formulations have been marketed for a long time. In fact, carbonates and silicates form part of many formulations containing phosphates. However, formulations based primarily on carbonate/silicate appeared on the market in response to publicity given to the lake-enriching effect of phosphates. Unfortunately, some smaller producers marketed "dry mix" detergents which were hazardous to the consumer by ingestion or eye contact due to their strongly alkaline properties. It was partly on the basis of this hazard that the U.S. Surgeon General advised against a detergent phosphorus control program.

CITRATE-BASED DETERGENTS

Citrate-based detergents have had limited distribution until now. However, recent research (Schwartz 1972) has shown that when formulated with a suitable surfactant, citrate-based laundry detergents can usually be as effective as phosphate-based products. There is a cost disadvantage, but this may be eliminated by a proposed new process for producing commercial-grade citrate. Because citrate is a natually occurring substance which biodegrades rapidly, most scientists feel there will be no adverse public health or environmental effects from its widespread use in detergents. Studies at C.C.I.W. on effects on algal growth tend to confirm this view (Glooschenko and Moore 1972).

NITRILOTRIACETIC ACID (NTA)

Nitrilotriacetic acid is a synthetic chelating agent with many properties similar to phosphate as a detergent builder. Its use as an additive to improve phosphate formulations has been considered for many years. A major shift to NTA as a laundry detergent builder would result in the introduction of many millions of pounds of this synthetic material into the environment every year. Because of a fundamental concern for such large use of a synthetic substance, a major research program was launched to assess the impact of NTA on public health and the environment.

Fortunately, the public health and environmental effects of NTA had been researched for many years prior to 1970 by detergent manufacturers. These tests concentrated on biodegradability and acute toxicity. In recent years more concern has been expressed for sublethal effects such as carcinogenicity, mutagenicity, and teratogenicity, as well as environmental effects on biota and algal production.

Government scientists in Canada, the United States, and Sweden developed research programs on NTA when it became apparent that this substance was likely to become a major phosphate replacement in detergents. Meetings of scientists from the three countries were held at the Canada Centre for Inland Waters in December 1970 and October 1971 to exchange research information. There were also industry–government meetings in each country to exchange research data.

On the basis of available research data, each country established its own policy for the use of NTA in detergents. Canada and the United States have followed somewhat divergent paths. In December 1970, fall of 1971, and spring of 1972 the U.S. Surgeon General disapproved the use of NTA in detergents. Canada, however, has allowed the use of NTA, while not endorsing it or any other substitute.

A major Canadian monitoring program was initiated in the fall of 1971 to measure the NTA levels in environmental systems under the relatively limited NTA usage in Canada at that time. Lake, river, coastal, and ground waters were analyzed. It was believed that a winter program would yield data reflecting lowest rates of degradation, and, therefore, the highest environmental concentrations, especially as acclimation of bacteria to NTA might not be complete at this time. The monitoring program was designed to permit prediction of environmental concentrations if NTA became a full-scale replacement for phosphates.

The river water monitoring was performed in two regions: Winnipeg (Freshwater Institute, Environment Canada) and southern Ontario. In Ontario it was undertaken by the Procter and Gamble Company of Canada Limited. It was designed to include municipalities of various sizes (e.g. Brantford, Guelph, Kemptville), with various types of sewage treatment systems including lagoons, trickling filter, and activated sludge. Some municipalities had only primary treatment; one had a tertiary treatment system. Rivers were sampled above and below the effluent outfall, and sewage plant influent and effluent were sampled. Tap water from each community was also analyzed.

Marine waters nearshore were sampled on the Atlantic and Pacific coasts. One sample from Halifax Harbour showed a just-detectable (10 ppb) level of NTA. Groundwater samples were obtained from selected wells in eastern Ontario and southern Manitoba. Other locations were considered, but no likelihood of groundwater contamination was evident and sampling efforts were not justified. The only groundwater samples found to contain appreciable concentrations of NTA were also seriously contaminated by bacteria of sewage origin and unfit for human use on that basis.

As a result of research assessments and monitoring, it was determined that probable concentrations of NTA in the environment after full-scale replacement for phosphates would still be well below that which would cause concern for human and environmental health. Thus the government decided to require a further reduction in phosphates to 5% (as P_2O_5) on January 1, 1973.

The increase in NTA usage due to detergent phosphate controls requires a continuing monitor program. Selected environmental systems continue to be investigated to determine the pathways and fate of NTA. A nation-wide sampling including drinking water from a variety of sources has been established. Thus it is possible to monitor human intake and observe if there is any significant increase in NTA levels due to increased usage. To date there has been no significant increase in NTA concentrations in drinking water nor any observable changes in trace metal concentrations in lakes, rivers, or drinking water. In fact, almost all samples analyzed in 1973 for NTA gave values below the detection limit of 10 ppb.

The great phosphate debate (Legge and Dingeldein 1970; Vallentyne 1970) and the search for alternatives to phosphates acceptable from health and environmental points of view is a fascinating story of interaction of environmental research, public attitudes, and government action. It deserves a more extensive treatment at some future time.

Future Trends

Future trends in the form that lake studies will take in Canada are somewhat difficult to predict. However, the study just completed on the Okanagan Lake system in British Columbia may point the way to future developments (Anon. 1973). Four significant features of this study are: 1) It involves agencies of several levels of government, and university and private sector researchers. 2) It is fully comprehensive in its approach. The titles of the first set of public reports issued in 1972 illustrate this point. They are: a) "Water supply in the Okanagan Basin and operation of the Okanagan flood control works," b) "Water quality in the Okanagan Basin," c) "Limnology of the mainstream Okanagan lakes," d) "Land use and water demand," e) "Recreation and esthetic resources," and f) "Fisheries in the Okanagan Basin." Water quality issues and water quantity are being considered together; scientific inputs come from specialists that include meteorologists, sediment geochemists, microbiologists, and social scientists. 3) There has been a deliberate effort to ensure public participation in the decision-making process. A significant part of program funds has been devoted to keeping the public informed of the problems and results of the studies, and in obtaining feedback from the public on their wishes concerning water and lake management in the Basin. 4) Study planners were determined not to delay implemention of experimental pollution abatement measures. When preliminary indications suggested the need for facilities such as those for nutrient removal at Penticton, action was undertaken without awaiting completion of all the lake and environment studies.

The real challenge to scientists and engineers is to combine these features with scientific work of the highest quality to ensure wise management of our lakes for future generations.

Acknowledgments

Much of the statistical information in the first section of this paper was drawn from unpublished draft studies on national water needs compiled by the staff of Inland Waters Directorate, Ottawa. Permission to use the information is gratefully acknowledged.

Bruce, J. P. 1973. The role of research in lake management. Proc. Symp. on the Lakes of Western Canada, Water Resources Centre, University of Alberta, Edmonton, Alta. p. 8–24.

Dobson, H. H., and Gilbertson. 1971. Oxygen depletion in the hypolimnion of the central basin of Lake Erie, 1929 to 1970. Proc. 14th Conf. Great Lakes Res. p. 743–747.

Gilbertson, M., H. H. Dobson, and T. R. Lee. 1972. Phosphorus and hypolimnial dissolved oxygen in Lake Erie. Project Hypo. Canada Centre for Inland Waters, Paper No. 6; U.S. Environ. Prot. Agency Tech. Rep. TS-05-71-208-24: 141–144.

Glooschenko, W. A., and J. E. Moore. 1972. The effect of citrate upon phytoplankton in Lake Ontario. Symp. Bioassay Techniques in Environmental Chemistry. 162nd Natl. Meet., Am. Chem. Soc., Washington, D.C. 13 p.

Legge, R. F., and D. Dingeldein. 1970. We hung phosphates without a fair trial. Can. Res. Dev. Mag. March/April 19: 19–27.

Anon. 1970. Pollution of lakes Erie, Ontario, and the international section of the St. Lawrence River. International Joint Commission, Queen's Printer, Ottawa. 184 p.

1971. 1969 vacation trends and recreational patterns. Can. Gov. Travel Bur., Dept. Ind. Trade Commer. Queen's Printer, Ottawa.

1972. Great Lakes water quality agreement, Canada and the United States of America, signed at Ottawa, April 15, 1972. U.S. Gov. Printing Office, Washington, D.C. 69 p.

1973. Findings and recommendations of the consultative board under the Canada–British Columbia Okanagan Basin agreement. Dept. Environ., Ottawa.

Burns, N. M., and C. Ross. 1972. Project Hypo — an intensive study of the Lake Erie Central Basin hypolimnion and related surface water phenomena. Canada Centre for Inland Waters, Paper No. 6; U.S. Environ. Prot. Agency Tech. Rep. TS-05-71-208-24: 182 p.

Denison, P. J., and F. C. Elder. 1970. Thermal inputs to the Great Lakes 1968–2000. Proc. 13th Conf. Great Lakes Res., Int. Assoc. Great Lakes Res. p. 811–828.

Montreal Engineering Co. Ltd. 1971. Thermal inputs into Canadian waters 1970–2000. Contract study for Environ. Can. and Dept. Energy, Mines Resour. 89 p.

Pimlott, D. H., C. J. Kerswill, and J. R. Bider. 1971. Scientific activities in fisheries and wildlife resources. Science Council of Canada. Special Study 15. 191 p.

Prince, A. T., and J. P. Bruce. 1972. Development of nutrient control policies in Canada, p. 433–446. *In* Allen and Kramer [ed.] Nutrients in natural waters. John Wiley and Sons, New York, N.Y.

Schwartz, A. M. 1972. Development of a heavy duty phosphate-free detergent. The Gillette Company Research Institute, Rockville, Md. Interim Rep. for Environ. Prot. Agency Contract FWQA 14-12-875.

Shiomi, M. T., and K. W. Kuntz. 1973. Great Lakes precipitation chemistry: Part I. Lake Ontario basin. Presented at 16th Conf. Great Lakes Res., Int. Assoc. Great Lakes Res. p. 154–155.

Vallentyne, J. R. 1970. Phosphorus and the control of eutrophication. Can. Res. Dev. Mag. May/June 36: 36–49.

Vollenweider, R. A. 1968. Scientific fundamentals of the eutrophication of lakes and flowing waters, with particular reference to nitrogen and phosphorus as factors in eutrophication. Organization for Economic Cooperation and Development (OECD) Tech. Rep. Ref. DAS/CSI/68.27., Paris. 159 p.

Limnology and Education in the Next Decade[1]

J. R. VALLENTYNE

Department of the Environment
Fisheries and Marine Service
Freshwater Institute, Winnipeg, Man. R3T 2N6

VALLENTYNE, J. R. 1974. Limnology and education in the next decade. J. Fish. Res. Board Can. 31: 513–519.

The prime environmental contingency affecting Canadian limnologists and limnology during the next decade may be a deteriorating economic situation brought about by global demophoric (population × technology) growth. In such an event there would be strong pressure for a fusion of economic and ecological interests, and for organizational arrangements facilitating problem solving. As an adaptation of this fusion, arguments are presented for cooperative education in which students with different disciplinary backgrounds jointly conduct problem-oriented work.

VALLENTYNE, J. R. 1974. Limnology and education in the next decade. J. Fish. Res. Board Can. 31: 513–519.

Le principal imprévu environnemental qui affectera la limnologie et les limnologistes canadiens au cours de la prochaine décennie pourrait être une situation économique en voie de détérioration par suite de la croissance démophorique (population × technologie). Dans une telle éventualité, il y aurait forte pression vers la fusion des intérêts économiques et écologiques, et vers l'agencement des corps organisés pour faciliter la solution des problèmes. Comme adaptation à cette fusion, nous mettons de l'avant des arguments en faveur d'une éducation coopérative selon laquelle des étudiants formés à différentes displines poursuivraient en commun des travaux orientés vers ces problèmes.

Accepted October 2, 1973

> *The depersonalization of the individual gives way to a process which is so far-reaching that it makes adaption to new criteria of life extremely difficult. It is a question of changing a tradition which has become thoroughly engrained in all our convictions and all our customs. It is a question of eliminating certitudes which have never been placed in doubt in the course of centuries.*
>
> UGO SPIRITO (1971)

THIS PAPER is addressed to the future. In preparing it I became convinced of three things: (1) that the trend from discipline-oriented work toward problem-oriented work will continue; (2) that my emphasis should be focused on the behavioral characteristics of limnologists rather than the subject matter of limnology, in that the former determine the latter rather than vice versa; and (3) that our educational system is outdated in terms of the almost exclusive accent on the individual as an autonomous unit.

The need for problem-oriented education in connection with environmental issues has been stressed by Steinhart and Cherniak (1969) and the Science Council of Canada (1973). It needs no further elaboration here. In this paper I have been more concerned with inventing a future environmental contingency and examining its probable consequences than I have with completeness of coverage and accuracy of prediction. My approach has been based on two major premises — that the future does not develop as a logical extension of the past, and that the development of limnology in Canada during the next decade will be more profoundly influenced by events external to the discipline than by those occurring within it. This is comparable to saying that terrain and climatic conditions can exert as much, if not more, influence on the evolution of transportation systems as vehicles.

The validity of these premises can be appreciated by comparing predictions that might have been made about Canadian limnology at the onset of the last decade with the actual events. I contend that if predictions based solely on limnological

---

[1] This paper, part of a special issue that comprises a comprehensive review of Limnology in Canada, was prepared to mark the 19th Congress of the International Association of Limnology (SIL), in Winnipeg, Man., during August 1974.

Printed in Canada (J3181)

experience had been made, they would have completely missed all the major innovations that took place. The innovations that appeared were not predictable from limnological knowledge alone; they could be foreseen only as consequences of anticipated environmental contingencies external to the discipline, and then only in a general way.

Limnology in Canada 1964–74

The principal environmental contingency that set the pattern for new limnological developments in Canada during the past decade was the public recognition of an environmental crisis which reached its peak in intensity during the latter part of the 1960s. The crisis was in large part an emotional reaction to the sudden appearance of symptoms indicative of technology out of control. Five names are sufficient to characterize the period: Silent Spring, Torrey Canyon, thalidomide, smog, and mercury. Collectively, these created an atmosphere that paved the way for sweeping changes in federal and provincial government departments, and increased attention to the consequences of accelerating technological growth. Some may legitimately question the adequacy of the changes that have taken place; but no one could deny that major changes have taken place and, for better or worse, that they have significantly modified the direction and content of limnology in Canada.

The principal limnological consequences that emerged as a result of the environmental crisis in the 1960s were the appearance of two major federal centers of limnological activity (the Canada Center for Inland Waters in Burlington, Ont., and the Freshwater Institute in Winnipeg, Man., Fig. 1 and 2, respectively); an increase in the number and size of industrial consultant groups involved in environmental impact assessments; and the initiation of several large-scale, multidisciplinary studies of major Canadian drainage basins. Among the latter, the following are most noteworthy: (1) studies on the pollution of the St. Lawrence Great Lakes under the International (Canada–United States) Joint Commission; (2) a joint federal–provincial study of the Okanagan Basin in British Columbia in connection with future growth and development; (3) a joint federal–provincial study of Lake Winnipeg and the Churchill and Nelson rivers in Manitoba, relative to hydroelectric power development; (4) federal and industrial studies on northern drainage systems relative to proposed oil and gas transport routes; (5) a joint Canada–United States study of pollution in the St. John River Basin under the aegis of OECD (Organization for Economic Cooperation and Development). The Canadian IBP (International Biological Program) work on Char Lake and Marion Lake, and the Experimental Lakes Area studies described elsewhere in this issue might be added to the above; however, they differ from the others in the lack of direct socioeconomic involvement.

I do not claim that the above were the only significant developments in Canadian limnology during

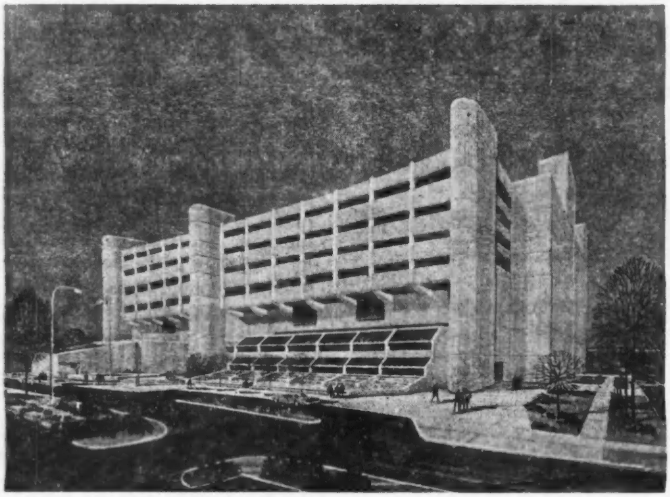


FIG. 1. Central research and administration building of the Canada Centre for Inland Waters, Burlington, Ont. (Architect's sketch)

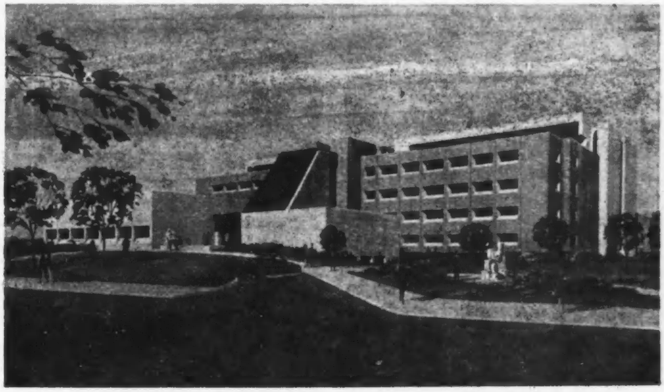


FIG. 2. Freshwater Institute building in Winnipeg, Man. (Architect's sketch)

the past decade, or that any or all of them have evolved in the best manner from an overall point of view. My only contention is that they were new and unexpected, that Canadian limnologists were not prepared for them when they came, and that they have exerted and will continue to exert a considerable influence on Canadian limnology and limnologists in the future.

What is the significance of these innovations and how have they affected us in terms of our attitudes and behavioral patterns? Their principal characteristics are so obvious that it seems superfluous to cite them: a shift from discipline-oriented work to problem-oriented work; involvement in complex questions demanding resolution of conflicting social desires; cooperative, multidisciplinary approaches to achieving socially acceptable syntheses; and an accent on environmental impact assessments. The terms problem-oriented, environmental impact, multidisciplinary, and social have become so much a part of our contemporary jargon that we take them for granted more than we should. Although many limnologists have doubtless just shifted their vocabulary to incorporate the new terms, I am convinced that there has also been a statistical change in the attitudes and behavioral patterns of limnologists in regard to the concepts behind these words, in part due to the influx of new personnel, new sources of funding, and perhaps a desire to contribute to what were previously social, economic, and political decisions.

As one measure of the increase that has taken place in collaborative work, Fig. 3 shows the trend over the past 70 yr in mean number of authors per paper published in the *Journal of the Fisheries Research Board* and more recently *Limnology and Oceanography*. Although I am sure that some of this change merely reflects an increase in democratic attitudes, part of it must also signify a need for cooperative interaction among specialists in an age of increasing specialization. I believe we have only just begun to explore the possibilities inherent in cooperative interaction and concur with Brown (1971) that further progress is unlikely to occur until we have a better description and understanding of organizations.

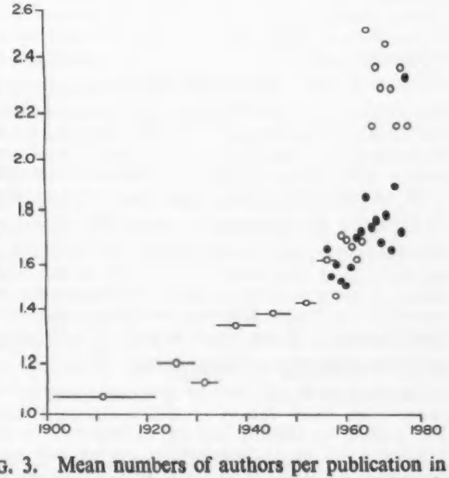


FIG. 3. Mean numbers of authors per publication in the *Journal of the Fisheries Research Board of Canada* (open circles 1901–72) and *Limnology and Oceanography* (closed circles 1956–72). Early issues of JFRBC were grouped because of the low numbers of papers per year; otherwise the data are for calendar years.

Limnology in Canada 1974–84

On the basis of the previous section, the best approach to predicting the future course of Canadian limnology should come from a consideration of future environmental contingencies expected to arise externally to the discipline. I will simply invent one anticipated future contingency without any serious attempt at documentation other than to say that I consider it likely to arise during the next decade. Those who wish to take issue with my invention can negate it simply by disregarding it. I am making no claim to any special abilities in clairvoyance. If my prediction turns out not to be the case, so much the better; if future events corroborate it, we may be better prepared for it than we would otherwise have been.

I believe the next decade will be characterized by adverse economic conditions relative to present economic projections and that these will have major repercussions on limnologists and limnology. My reasons for this belief are based on the high and accelerating momentum of global demophoric (population × technology) growth and the probability of organizational breakdowns during the terminal phases of exponential growth in a finite global environment (Vallentyne 1972, 1973). Present indications of a disparity between energy "needs" and supply suggest a possible causal mechanism.

The consequences of a deteriorating economic situation would be an increased accent on problem-oriented work promising rapid, short-term solutions, a continuation of the current downward trend in support of basic research, a relaxation of environmental quality standards, and an accent on jobs and urban environments rather than on recreation and wild environments. The overall trend would be away from an ecological point of view and toward the traditional economic point of view, linking jobs and economic growth. My only claim is that these consequences are likely to take place in the event of deteriorating economic conditions, not that they would necessarily be adaptive or beneficial. On the contrary, I would expect traditional economic solutions to be counterproductive, exacerbating an undesirable situation because of faulty assumptions on which a large part of current economic doctrine is based (Daly 1971).

My concern is not how to save limnology in the event that these future conditions should arise, but, rather, to identify the forces that will be impinging upon us as limnologists, so we can react to them in an adaptive fashion. If, for example, we were to align ourselves solely with the wild environment during a period of adverse economics, we would be following a self-defeating course. The situation would be analogous to a community of oligotrophic organisms fighting for survival under conditions of an increasing nutrient load.

To state this another way, there is likely to be a strong selective pressure during the next decade for a union of traditional economic and ecological points of view with a carry-over into political science as well. If ecologists do not participate in this process, it will proceed without them. Managers will not feel they can afford the luxury of waiting for ecologists to respond. The only center in Canada in which an effective ecological thrust is now being made into problem-oriented work involving social, economic, and urban considerations is the Institute of Animal Resource Ecology at the University of British Columbia. It is likely to provide most of the Canadian leadership that will be required in this area in the future.

Something more than merely thrusting economists, sociologists, and ecologists together is required to create the desired fusion of subject areas. There must be a predisposition toward collaborative, problem-oriented action and there must be a parallel development of organizational arrangements that enrich rather than inhibit (as is often the case) disciplinary and organizational interactions. For the latter, the interested reader can profitably consult Brown's (1971) lucid book *Organization.*

Part of the difficulty in uniting disciplines such as ecology and economics lies deeply imbedded in our educational system and the high selective value we place on specialization and individuals working in isolation rather than as part of a group. I have a proposal that might partially alleviate this difficulty. Before outlining it, it is necessary to appreciate the extent to which specialization and the increased flow of information have reduced our abilities as individuals to achieve meaningful syntheses of knowledge.

Syntheses and the Depersonalization of the Individual

In an article contrasting the need for synthesis in a world of increasing specialization, Spirito[2] concluded that in the 200 yr since Adam Smith first formulated the concept of the division of labor, the autonomy of the individual has been disappearing little by little, "giving way to a collective subjectivity which thinks and acts through continuous collaboration." Spirito had this to say about the impossibility of a science of synthesis: "In other words, synthesis can no longer be a synthesis of which a single science or a single scientist is capable, but it must result from the activity of all sciences through the collaboration of all scientists. Synthesis, therefore, is not lacking, but it forms endlessly, in the conscience of a subjectivity which is no longer able to conceive individually, for the simple reason that the individual no longer lives in his traditional particularity. Synthesis no longer exists because it is being created day by day through a process for which no single individual can be considered responsible........To find synthesis, we must move on the level of a historical process of becoming, which is achieving this synthesis above and beyond individuals, in a social life where no individual can hope to live totally."

---

[2] From "The interdisciplinary character of philosophy." Presented at a meeting of the Italian Society of Biology and Morals in Ottawa, Canada, spring 1971. (Seen as a manuscript only.)

I believe that in the next decade we will be faced with an increasing number of problems demanding synthetic views of reality and that we may be ill-prepared to solve these problems because of our educational preoccupation with the importance of the individual working in isolation. The tendency of both individuals and organizations to adopt territorial defense mechanisms may prevent us from achieving the synthesis necessary to bring about solutions in problem-oriented work.

Two examples pertaining to the Great Lakes Basin may help to clarify what I mean. Practically every scientist working on Great Lakes problems I have talked to is convinced that the Great Lakes Basin is headed toward economic and environmental decline as a result of uninhibited demophoric growth. Yet, these same scientists continue to work in their specialties, fully aware they are merely quantifying the signs of problems rather than treating the ultimate causes. They do this in part because of organizational limitations imposed on them and (in accordance with the principle of the division of labor) the knowledge that they would be less effective if they moved outside the areas of their specialties.

At a research organizational meeting I recently attended, it was proposed that research be undertaken to determine how the relation between water quality and land-use patterns might be better explained to inhabitants of the Great Lakes Basin. The comment was made that this was really not research, and for that reason should not be considered by the particular group meeting at the time. It reminded me of the story of a woman who was admonished by an usher in a high Anglican cathedral for periodically shouting hallelujas during the rector's sermon. "But, I've got religion!" she told the man. "I'm sure you have, madam," he whispered in reply, "but this is hardly the place for it."

In terms of synthesis and problem solving there is a fundamental distinction between discipline-oriented and problem-oriented work that is not commonly appreciated. In discipline-oriented work persons who possess erroneous conceptions of science or nature can, with profit, be ignored; in problem-oriented work they typically constitute the problem. The shift from discipline-oriented work to problem-oriented work is, therefore, not likely to be achieved either rapidly or comfortably; it involves a fundamental change in philosophy and approach.

As a result of the increasing need for ever-widening syntheses of knowledge in a problem-oriented context, an increased selection pressure is likely to develop in the next decade for specialists pre-adapted to work in groups. There should also be a corresponding selective advantage for the invention and evolution of organizational arrangements favoring rather than inhibiting solutions to social problems (Brown 1971). Yet, we are ill-prepared for such changes. Our educational system is almost exclusively devoted to teaching and assessing individuals on the basis of work conducted in isolation. It is as though we have been training players for individual roles on football teams without ever subjecting them to experience in cooperative play, creating soloists for a world in which orchestration is the rule, soliloquists for an audience that prefers Shakespearian drama. I believe the selective barriers to group activities in our educational system should be modified not only to permit, but to actively encourage, the development and recognition of cooperative work undertaken jointly on a group-survival basis by two or more individuals with different disciplinary backgrounds.

My particular concern is with the development of favorable links between ecology and economics in the resolution of social problems. The traditional way to deal with such matters has been to create interdisciplinary institutes and train interdisciplinary students. I believe this is the wrong way to go about things. It is comparable to creating nonreproductive hybrids from two species based on a blending type of inheritance. My proposal is to link specialist roles in facultatively mutualistic relationships, with the component "genomes" maintained in individuals. This leads me to suggest the cooperative thesis as one mechanism to aid in the development of synthetic group behavior.

Cooperative Education

Our educational system is designed to reward individuals for work performed in isolation. This is exemplified by the custom of assigning individual marks based on examinations. Although I do not question the utility of this approach, I do question whether it alone will be sufficient to produce graduates able to cope with the demands of future society. I believe a new selective framework must be developed to encourage student involvement in complex problem-oriented work, with rewards given to individuals on the basis of mutualistic interaction. I think that the two systems can proceed in parallel within a given institution and that both should be fostered at all levels of university education up to and including the Ph.D. thesis. The following remarks on the cooperative thesis as an example of cooperative education could pertain to any interaction of a lesser nature.

The Cooperative Thesis

The notion of the cooperative thesis came to me early in the preparation of this paper. When I found that three cooperative theses were in preparation at Cornell University, that cooperative theses are not at all uncommon in engineering schools in Poland (K. Patalas, Department of the Environment, Fisheries and Marine Service, Freshwater Institute, Winnipeg, Man., personal communication), and that quasi-cooperative theses (in sociology) have been undertaken in Canada, I became convinced that the idea was worthy of analysis and development.

The cooperative thesis as I propose it is as follows. It is a problem-oriented thesis undertaken jointly by two or more students under the direction of a committee of supervisors in the disciplines involved. The disciplinary backgrounds of the students should overlap minimally if the benefits of the interaction are to be maximized. The preparation and defense of the thesis is undertaken mutualistically on a joint pass-fail basis. If educational institutions require a distinction between students who have fullfilled degree requirements through cooperative versus individual theses, this could be done with recognition given to cooperants as members of a specific unit. My suggestion would be to limit the number of cooperants to two initially and to accent cooperative work at the undergraduate level as much as in graduate school programs.

The advantage of the cooperative thesis to students is that they would be able to feel a sense of involvement in challenging, problem-oriented work and would be able to interact with a second discipline without having to fulfil all the prerequisites typically required to establish competence in a field. Equally important from both professorial and student points of view, each cooperator would individually be required to develop the same degree of competence in his professor's specialty as students involved in individual theses. The advantage to the professors is that they could serve a useful educational function in terms of training students in meaningful problem-oriented work without sacrificing professional (disciplinary) standards. The advantage to the sponsoring institution would be a more rapid adaptation to new interdisciplinary needs of society.

In discussing the notion of cooperative theses with some colleagues I have encountered both support and opposition. I believe that much of the opposition stems from the fact that, having been trained under one system, we find it difficult to conceive of another so dramatically different in its foundations.

Cooperative Theses in Canada

I wrote to 18 Canadian graduate schools asking if cooperative theses were permissible and how many had been completed in the past 5 yr. The 14 replies are tabulated below. In the two instances where a significant number of quasi-cooperative theses were undertaken, the theses were all on sociological topics.

Graduate school	Permitted	Completed in last 5 yr
Dalhousie University	no[3]	some[3]
McGill University	yes	none
McMaster University	no	none
Simon Fraser University	yes	several
University of Alberta	yes	none
University of British Columbia	no	none
University of Calgary	no	one[4]
University of Guelph	yes	none
University of Manitoba	no	none
University of New Brunswick	no	none
University of Ottawa	no	none
University of Toronto	no	none
University of Waterloo	no	none
University of Western Ontario	no	none

Conclusion

This paper will not be very appealing to contemporary limnologists because of its futuristic advice to specialists and lack of technical content. My hope is that it may be read by students preparing to enter the discipline, for their behavior will be shaped by the future.

---

[3] Some cooperative theses were undertaken in a School of Social Work prior to its conversion into a university department.

[4] Allowed to proceed as an exception to the rule.

BROWN, W. 1971. Organization. Heineman Educational Books Ltd., London. 400 p.

DALY, H. E. 1971. Toward a stationary state economy, p. 226–244. *In* J. Harte and R. H. Sokolow [ed.] The patient earth. Holt, Reinhart and Winston, New York, N.Y.

SCIENCE COUNCIL OF CANADA. 1973. Natural resource policy issues in Canada. Sci. Counc. Rep. No. 19: 1–40.

STEINHART, J. S., AND S. CHERNIAK. 1969. The universities and environmental quality — commitment to problem-focussed education. A report to the President's Environmental Quality Council. Off. Sci. Technol. U.S. Government Printing Office, Washington, D.C.

VALLENTYNE, J. R. 1972. Freshwater supplies and pollution: effects of the demophoric explosion on water and man, p. 182–211. *In* N. Pulunin [ed.] The environmental future. Macmillan, and Co., London. 670 p.

1973. New term introduced at First Conference on Environmental Future. Biol. Conserv. 4: 371–372.

Impact of Recent Economic Growth and Industrial Development on the Ecology of Northwest Miramichi Atlantic Salmon (*Salmo salar*)[1]

PAUL F. ELSON

Department of the Environment
Fisheries and Marine Service, Biological Station, St. Andrews, N.B.

ELSON, P. F. 1974. Impact of recent economic growth and industrial development on the ecology of Northwest Miramichi Atlantic salmon (*Salmo salar*). J. Fish. Res. Board Can. 31: 521–544.

The history of Atlantic salmon (*Salmo salar*) runs of the Northwest Miramichi from 1950 to 1973 is reviewed. Decreases in these runs are related to degrading of ecological conditions in the river's rearing reaches as a result of adverse chemical conditions attributable to recent developments in forest management and to base metal mining. Diversion of indigenous adult stocks into other streams of the system as a result of pollution of the home stream by mining, pulpmill, and other human activities is examined and evaluated. Increase of commercial catches as a result of pollution-caused delay in the estuary of migrating adults is analyzed. Grave depletion of stocks as a result of the combined effects of these factors plus distant-water fishing is identified, as is incipient recovery of stocks when home-water commercial fishing was eliminated and pollution abatement measures were introduced to the river. A suppressing effect of heavy angling pressure on stock abundance when stocks are low is noted.

ELSON, P. F. 1974. Impact of recent economic growth and industrial development on the ecology of Northwest Miramichi Atlantic salmon (*Salmo salar*). J. Fish. Res. Board Can. 31: 521–544.

Nous faisons l'historique des montaisons de saumons atlantiques (*Salmo salar*) dans la Miramichi Nord-Ouest de 1950 à 1973. Le déclin de ces montaisons est lié à la dégradation des conditions écologiques dans les secteurs d'alevinage de la rivière, résultat de conditions chimiques défavorables que nous attribuons aux récentes pratiques de gestion forestière et à l'exploitation minière des métaux de base. Nous examinons et évaluons le détournement des stocks adultes indigènes vers d'autres cours d'eau du régime, à la suite de la pollution de la rivière natale par les opérations minières, un moulin de pâte à papier et autres activités humaines. Nous analysons l'augmentation des prises commerciales produite par un séjour plus long dans les estuaires, imposé par la pollution aux adultes en voie de migration. Nous reconnaissons un déclin sérieux des stocks dû aux effets combinés de ces facteurs, de même qu'un début de récupération, une fois la pêche commerciale interdite dans les eaux indigènes, et des mesures de réduction de pollution introduites sur la rivière. Nous soulignons l'effet dissimulateur qu'une forte pression de pêche à la ligne exerce sur l'abondance des stocks, lorsque ceux-ci sont à un bas niveau.

Accepted December 17, 1973

ATLANTIC salmon (*Salmo salar*) have been and still are considered one of the most desirable anadromous fishes associated with the rivers and coasts of the North Atlantic region. To comprehend the potential of local industrialization for degrading its environment, the salient points of its life history must be understood. Atlantic salmon must breed in cool, clean, swift, freshwater streams, spend the first 2–4 yr of their life there as parr, pass seaward through estuaries as smolts, make most of their growth in the next 1 yr (grilse) to 3 yr (salmon) in near or distant ocean waters, then return to their breeding streams. Few (only 5–10%) spawn more than once. Jones (1959) describes the life history and biology.

Demand for Atlantic salmon as a choice food has been high throughout history and has increased in recent decades (Netboy 1968; Chung 1973).

---

[1] This paper, part of a special issue that comprises a comprehensive review of Limnology in Canada, was prepared to mark the 19th Congress of the International Association of Limnology (SIL), in Winnipeg, Man., during August 1974.

Printed in Canada (J3248)

Salmon are also the basis for important recreational fisheries: angling for returning adults in their rivers of origin. Catering to anglers is also an important industry on the better angling rivers. In common with other forms of recreation, demand here, too, is increasing (Hooper and Hustins 1973; Netboy 1968).

A measure of the increase in utilization of the species is provided by increased world landings (commercial plus recreational) from an average of 8374 metric tons for the 5 yr 1960–64, to 10,353 tons for 1968–72, an increase of 24% (data from ICNAF 1973).

This paper examines drastic declines in Atlantic salmon production from the Northwest Miramichi River (Fig. 1) between 1950 and 1971, and the beginnings of recovery in 1972 and 1973. The recovery is associated with remedial measures applied to practices inducing environmental debasement and to fishing pressure which, though little changed, became excessive for the depleted stocks.

Sources of Data

The Northwest Miramichi drainage basin comprises about one tenth of the total Miramichi basin. Up to the early 1950s it probably provided at least one tenth of Miramichi salmon production and thus should serve as a more or less valid sample of trends in Miramichi stocks as a whole.

A fence and traps to facilitate counting ascending and descending migrant salmon, about 11 km (7 miles) above tidehead on this stream (position indicated in Fig. 1), have been maintained since 1950 (Kerswill 1971). Fish movements could be associated with such environmental variables as water flow, temperature, and other qualities. Proportionate exploitation of Northwest salmon in different fisheries was studied by applying distinctive finclips (1950–61) or serially

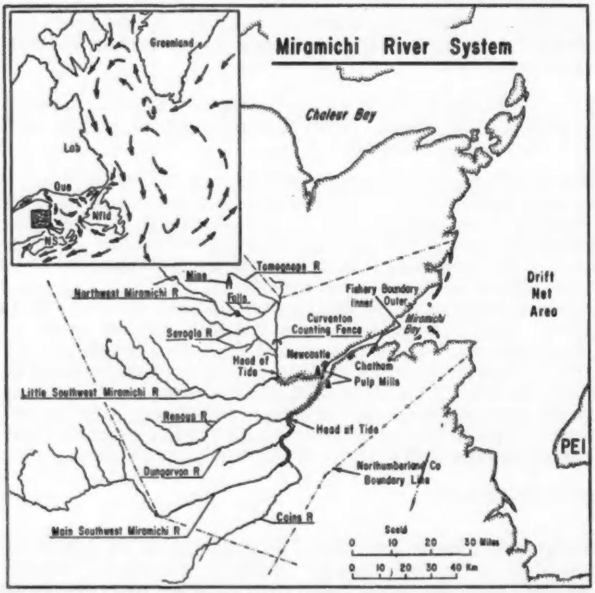

Miramichi River System
Greenland
Lab
Que
Nfld
NS
Chaleur Bay
Tomogonops R
Mine
Northwest Miramichi R
Falls
Fishery Boundary
Inner
Outer
Curventon
Counting Fence
Miramichi Bay
Sevogle R
Head of Tide
Newcastle
Chatham
Pulp Mills
Little Southwest Miramichi R
Renous R
Head of Tide
Drift Net Area
PEI
Dungarvon R
Northumberland Co Boundary Line
Cains R
Main Southwest Miramichi R
Scale
0 10 20 30 Miles
0 10 20 30 40 Km

FIG. 1. The Miramichi River system and its location (dotted square in the insert) on the Atlantic coast of Canada. Arrows in the insert show general direction of oceanic currents of the region, which may assist in distribution of some Northwest Miramichi salmon to distant waters. Demarcation between outer (Fishery Districts 70, 73) and inner (Districts 71,72) segments of the commercial salmon fishery is shown. Angling occurs throughout the main branches of the system from the head of tide up, as well as in some of their larger tributaries. The falls on the Northwest Miramichi River is used as the arbitrary division between upper and lower reaches of this stream.

numbered tags (1959–73) to a large portion of descending smolts intercepted at the counting fence. Records of total catches in commercial and recreational fisheries, as well as recaptures of marked fish, were made available through cooperation of officers of the Canadian Fisheries Service. Annual assessments of recruitment of young of the various year-classes were made by electrofishing (Elson 1962a,b; 1967). Thus relations between exploitation of the stocks by marine and estuarial fisheries, by angling in the river, and escapement could be related to subsequent recruitment of young.

On-site residence of competent field staff responsible for counting fence operation, electrofishing, and collection of marks and tags from fishermen assured alertness to conditions in river and local fisheries, and this was augmented by frequent visits of supervising scientists.

To relate salmon movements to environmental parameters, particularly those affected by industrialization, the technique of simple statistical correlation has been drawn on heavily.

A number of analyses pertinent to the present subject and using earlier data from the same sources have already been published. For the sake of interpretive clarity reference to them is made under appropriate subject headings.

Results and Discussion

CHARACTERISTICS AND TRENDS OF THE STOCKS ENTERING THE RIVER

The impact of environmental changes brought by recent industrial developments to Northwest Miramichi salmon must be examined in the context of the nature of the stocks. The total stock appears to have at least four basic components. These are early-running grilse and salmon and late-running grilse and salmon. Saunders (1967) showed that most mature fish going to the upper reaches to spawn had in fact come from there as smolts.

Tag returns from fish tagged as native smolts and caught by anglers above the fence (1964–73) indicate that 15% of the tagged grilse and 18% of the tagged large salmon liberated above the fence were caught. But creel census and fence counts indicate that 39% of all grilse and 52% of all large salmon passing up by the end of August were caught. Average annual exploitation of total populations was 18% as measured by tag returns and 31% as measured by creel census and fence counts. Thus, a correction factor of 72% would have to be added to the exploitation rate measured by tags to give the same rate as that measured by creel census and fence counts. Moreover, these fish entered the river noticeably earlier in the year than did those constituting the late run, which spawned in the lower eraches of the river. Møller (1970) and Payne et al. (1971) have established that there are genetically different groups of salmon in different but adjacent areas. Using Møller's technique it was not possible to firmly establish genetic differences between parr from the upper reaches vs. those from the lower reaches of the Northwest Miramichi. However, esperiments involving liberation of tagged, hatchery-reared smolts from selectively bred Northwest Miramichi salmon (early grilse × early grilse, early salmon × early salmon, late grilse × late grilse, late salmon × late salmon) have given some insight (Elson 1973a). More grilse than salmon were recaptured from grilse matings and more salmon than grilse from salmon matings. Moreover, the progeny of early-run fish, both grilse and salmon, entered the freshwater reaches of the home river about 2 mo earlier, on average, than the progeny of late-run fish. In the above experiments early-run parents qualified by reaching the counting fence by July 15, and late-run parents reached the counting fence in comparatively bright condition only after August 31. Normally, there is little upward movement of salmon in this river during August (Saunders 1967).

The trends observed for the four different stock components are illustrated in Fig. 2. All grilse and salmon that ascended to the counting fence by August 31 are considered throughout this paper as contributing to the early, or summer run because they are available to anglers; those entering from September 1 on are regarded as late-run. Early-run grilse have maintained their river population moderately well and so have late-run grilse except for the 1969 and 1971 year-classes. The larger salmon, the only lawful target for home commercial fishermen (within 80 km (50 miles) of the estuary), have fared less well since the early 1960s. Early-run salmon, which escaped some of the commercial fishery, have maintained their numbers better than late-run salmon that were vulnerable to the commercial fishery throughout most of the season. (In the selective breeding studies mentioned above, the commercial fishery reported about 40% of early-run, large salmon and 50% of late-run. Anglers took 8 and 5%, respectively.) The New Brunswick commercial fishery is not the only cause for decline and may even be a secondary rather than a primary contributing factor. That the home commercial fishery was a contributing factor is, however, shown by improved runs in 1972 and 1973, following a ban on all commercial salmon fishing in New Brunswick; grilse, too, benefited from the ban (Fig. 2).

EXPLOITATION IN FISHERIES

It may clarify matters to indicate what residuum of the overall stock is represented by the grilse and salmon ascending to the counting fence (Fig. 1 and 2) and later escaping to spawn, as well as how the overall production has been exploited each year. Information on this aspect is available through recaptures of wild smolts tagged as they descended past the counting fence. The data are illustrated in Fig. 3, where they are presented as percentage values of the total recaptures from each smolt year-class. The data are not adjusted for nonreporting of tags, which was particularly bad in the West Greenland high seas fishery. There is considerable year-to-year variation in exploitation by different fisheries of the 12 smolt year-classes shown. Points of interest include variable commercial exploitation of grilse in Newfoundland (legal) and the home area (illegal), variable utilization of immature 2-sea-winter salmon in Greenland, utilization of 2-sea-winter salmon in the home commercial fishery, comparative use by anglers of both grilse and salmon, and escapement rates, especially for large salmon which are crucial for recruitment (Paloheimo and Elson 1973). Average percentage recaptures in various fisheries for smolts released in 1960–71 show a changed pattern from those for smolts released in 1950–61 as indicated by Kerswill's (1971) data (Table 1). Increased exploitation, especially of large salmon, is indicated; moreover, fisheries near or on spawning grounds began to get proportionately less than those farther out.

But while modern times have brought heavier fishing pressure on Atlantic salmon, pollution and other forms of environmental change have added or contributed to even more pressure on the species. Effects of various types of chemical pollution have been discussed in broad detail by Elson et al. (1973). Other forms of adverse environmental change associated with practices of the forest industry are noted in Elson et al. (1972b). Except

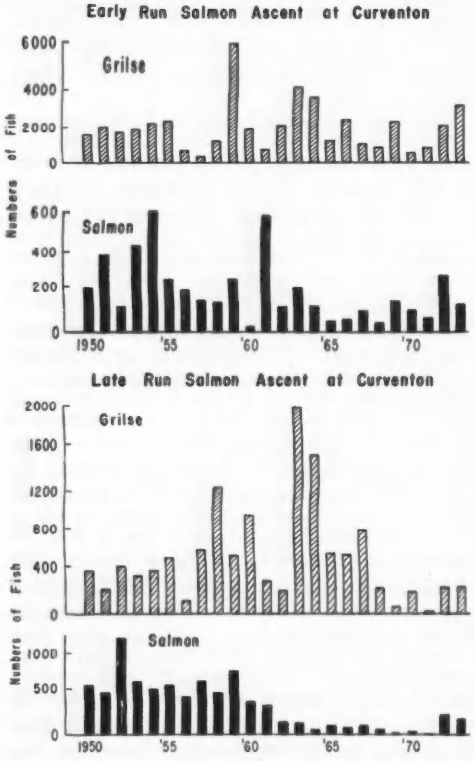


FIG. 2. Numbers of Atlantic salmon (*Salmo salar*) by sea age and season of entry, ascending the Northwest Miramichi to the counting fence at Curventon, 11 km (7 miles) above head of tide. Early run includes all those taken by August 31; late run, those taken after.

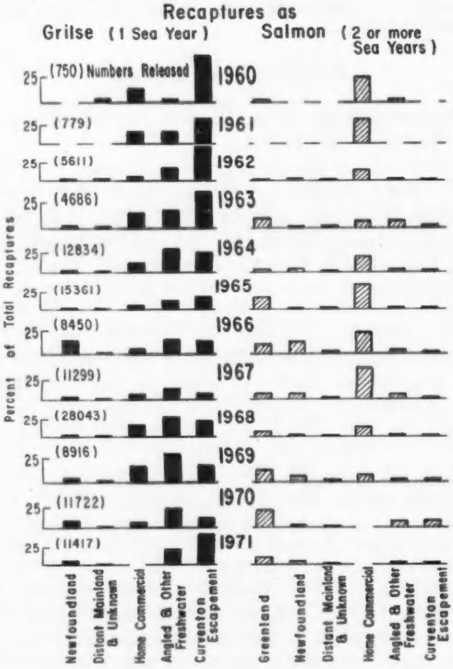


FIG. 3. Exploitation in various fisheries and escapement of grilse and salmon tagged as wild smolts when first migrating seaward past the counting fence on the Northwest Miramichi River: years of smolt release in center.

where new data or analyses are available these matters will be but briefly reviewed here.

FOREST MAINTENANCE AND HARVESTING

Beginning in 1952 aerial spraying of New Brunswick forests against insect pests has been almost an annual occurrence. The direct impact of this practice on salmon has been described in detail (e.g. Elson 1967; Kerswill 1967; Elson and Kerswill 1964, 1966) as well as summarized in general publications (Elson et al. 1972b, 1973).

Initially, DDT was the insecticide of choice. It sometimes killed over 90% of underyearlings and 50% or more of parr. Mortalities of young were reflected in numbers of returning adults. Spraying of DDT on the Northwest Miramichi occurred in 1954, 1956, and 1957. Some DDT was also applied on its lower basin in 1964. The river, in 1964, had a 0.4 km (0.25 mile) wide buffer strip of the much less damaging (Grant 1967) organophosphate insecticide phosphamidon applied along each bank. The slump in numbers of early-run salmon and grilse during the last half of the 1950s and early 1960s (Fig. 2) is attributable in large part to DDT. In the upper river most young salmon became smolts as 3-year-olds until the late 1960s (M. G. Forsythe 1967, 1968, and unpublished age data from electrofishing). Since then, perhaps in part because of reduced populations and less interspecific competition, the dominant smolt age has changed to 2 yr (unpublished data). The lower reaches used as rearing grounds by late-run fish produced a mixture of 2- and 3-yr smolts resulting in a population having more resilience against occasional catastrophe. This may partly account for less obvious early depression of the late-run stocks.

Besides the direct effects of DDT in killing young fish and their food organisms, it can induce adverse behavioral changes in salmonids involving, for example, response to temperature and reaction to stimuli causing avoidance and seeking of shelter (Anderson 1971). Experimental exposure of wild salmon smolts to DDT resulted in about 57% as many adult recaptures as from similarly handled smolts not exposed to DDT (Anderson and Elson 1971). Persistence of DDT residues in salmonids from streams of eastern Canada and Maine has been reported. In the Anderson–Elson experiment the treated smolts had DDT-and-metabolite residues (Elson et al. 1973) comparable to those found by Sprague et al. (1971) and Dimond et al. (1971) 1–3 yr after spraying. How small exposure to DDT would cause attrition of adult salmon runs has not received more investigation. But it seems not unreasonable to suppose that Northwest adult salmon populations suffered from such subacute dosage, perhaps by up to 40% attrition to 1960 and by decreasing amounts since.

There are indications that fenitrothion, far less damaging than DDT, may have a depressing effect on abundance of aquatic insects (food for parr) and perhaps on fish, too, particularly when applied in successive years (Elson et al. 1973). But most of the Northwest Miramichi was first exposed to this insecticide in 1973, so any possible impact on Northwest salmon runs is not yet evident.

Extensive cutting of forests of the Northwest Miramichi has had some adverse effects on the ecology of local salmon. In 1958, 6 yr before log driving ceased, low autumn river discharge delayed a large river-drive of pulp logs that had been dumped into the upper river and many salmon failed to reach headwater spawning areas. This was reflected in a local low population of underyearlings the following year (Elson 1967). Following the extensive cutting, the bed of the river became wider, shallower, comparatively clear of obstructions like fallen bank-side trees, and lost the many little deep pockets and pools between riffles (Elson et al. 1972b) that constitute the best habitat (Elson 1967) for young salmon. Such levelling of the stream bed (Table 2) almost certainly played its part in limiting production. Sparse spawning populations (Fig. 2) throughout the 1960s, and hence reduced need for a large area of ideal habitat, have prevented the full effect

TABLE 1. Change in percentages of total recoveries of marked or tagged Northwest Miramichi smolts in various fisheries and as escapement.

		Newfoundland		Home comm.		Anglers		Escapement		Percentage of total as	
Period	Greenland	grilse	salmon	grilse	salmon	grilse	salmon	grilse	salmon	grilse	salmon
1950–61 (finclips)	0	>1	5	7	39	8	3	22	13	38	62
1960–71 (tags)	9	4	4	10	18	19	4	27	2	62	38

TABLE 2. Changes[a] in some physical characteristics of the upper part of the Northwest Miramichi River following extensive forest harvest, compared to changes in lower part. (1 ft = 0.305 m)

	Upper part (five stations)				Lower part (three stations)			
	Width (*ft*)	Depth (*ft*)		Water temp (*C*)	Width (*ft*)	Depth (*ft*)		Water temp
		channel	pools			channel	pools	
Before cut (1951–57)	63	1.2	2.1	15.0	107	1.6	2.7	17.8
After cut (1965–71)	64	1.1	1.3	14.1	122	1.1	1.5	19.6
Change	+2%	–8%	–38%	–6%	+14%	–31%	–45%	+10%

[a] From yearly measurements at each end of sample areas used for assessing abundance of young; these eight sample areas used each year from 1951–1971.

of this levelling from appearing. On the upper reaches this cannot occur before 1974 and on the lower reaches until some years later. Kanid'ev (1968) found that it took 5–10 yr for rivers to recover from effects of bad forest practice. Bochkov (1970) reports the broad experience from European USSR that forest generally decreases the surface flow and runoff from small catchments but increases the minimum flow and usually increases the total annual flow from medium to large rivers. Changes noted for the Northwest Miramichi above seem bound to have some adverse impact on the ecology of resident salmonids.

BASE METAL MINING

Development of base metal mining has played an important part in the economy of New Brunswick during the last 20 yr. A copper–zinc deposit located on the headwaters of the Tomogonops River (Fig. 1), tributary to the lower Northwest Miramichi was given extensive exploration in 1954 and preliminary development in the next 3 yr. In 1960 sump water was pumped out of two shafts into the Tomogonops in June. Salmon which had ascended above the counting fence immediately began to drop back down, some in moribund condition. Association of the two incidents led to intensive research on the matter in following years. This is reviewed by Elson et al. (1973).

Sprague et al. (1965) and Saunders and Sprague (1967) describe decreases in bottom fauna and resident fish and fallback of uprunning adults below the source of pollution. About 60% of the fallbacks were not seen again. Pollution was most serious at times of heavy rainfall and runoff. Proportions of copper and zinc in the water varied from time to time but their effects were additive. So a system of expressing their combined effect as toxic units (1.0 TU = incipient lethal level for parr) was devised (Sprague and Ramsay 1965). Humic acid in the river water somewhat mitigated the effects as compared to those found in the laboratory (Wildish et al. 1971; Carson and Carson 1972). But concentrations above 1.0 TU were followed by death of many salmon and concentrations above 0.4 TU were usually accompanied by fallback of adults at the fence (see Fig. 5, *Upper*). Table 3 lists the number of days such concentrations were recorded each year. Confirmation that fall-

TABLE 3. Number of days at the Northwest Miramichi River counting fence with copper–zinc pollution, measured as Toxic Units, at or above level (0.4 TU) causing downstream movement and/or avoidance by uprunning salmon during season of run (May 16–October 15), angling season (May 16–August 31), and at or above level (1.0 TU) causing mortality to young salmon throughout the year.

	Avoidance by adults (≥ 0.4 TU)		Mortality to young (≥ 1.0 TU) (Jan 1–Dec. 31)
	Fallback at fence (May 16–Oct. 15)	Diversion into Sevogle (May16–Aug. 31)	
1960[a]	50[a]	49[a]	3[a]
1961[a]	19[a]	18[a]	0[a]
1962	72	61	6
1963	96	61	56
1964	41	35	33
1965	53	35	19
1966	14	14	34
1967	44	28	50
1968	4	4	8
1969	43	27	36
1970	15	10	9
1971	0	0	0
1972	0	0	0
1973	0	0	0

[a] Intermittent chemical analyses began on July 1, 1960; actual value measured in 1960, 6; 1961, 3; data tabulated is corrected to include all days with fallback at the fence; daily analyses from May 1962, on.

back was directly related to copper–zinc pollution comes from two experiments involving trucking adults from the fence to a liberation point in the Northwest about 15 km (9 miles) above the mouth of the Tomogonops. In July 1960, 24 tagged grilse were so translocated. Three were taken by anglers, 18 passed above a second counting fence 25 km (15.5 miles) farther up and the other three were unaccounted for but did not descend to the lower fence. Between June 10 and July 23, 1969, 90 tagged adults were similarly translocated. Sixteen were angled above the point of release. Two were reported as angled within a few days, well below the counting fence. But with consistent low water and negligible pollution between times of release and reported recaptures, it is unlikely that any of these fish could have gone downstream without being recorded at the counting fence; more likely they were taken illegally near the point of release, a favored area for poaching, and recapture locations reported incorrectly. None of the remaining 72 were subsequently reported. Once above the source of mainstem pollution, practically all fish stayed up. By 1970 recruitment of young was almost eliminated in the lower part of the river (see Fig. 14). By 1971 successful pollution abatement measures involving impounding and treatment with lime of all mine runoff water were instituted.

Besides fallback of adults, the copper–zinc pollution also caused more straying of native adults. Straying of returning grilse and salmon tagged as wild smolts descending the Northwest Miramichi can be best evaluated by examining where anglers caught such fish. Figure 4, *Upper*, shows this straying measured as percentages of the total catches by anglers (total numbers angled are also shown in the figure) made in other branches of the Miramichi system than the Northwest. The 1952–73 trend is one of increasing diversion described by a time-dependent regression fitted to the data of Fig. 4, *Upper* ($y = 1.22t + 10.55$, $P < 0.01$, where t = time).

Most of this straying occurred at two points on the return journey. A substantial proportion diverted from the Northwest stem at its confluence with the Sevogle (Fig. 1). The data are illustrated in Fig. 4, *Lower*; total number angled in the Northwest and Sevogle are also shown in the figure. Others had already turned into the Southwest arm of the estuary, as discussed in the next section, under "Processing forest products and urbanization."

Much of the straying into the Sevogle after 1960 is directly traceable to copper–zinc pollution of the Northwest. Impact of this environmental parameter was not recognized until 1960. But review of the history of exploration and development of the mine on the Tomogonops (Elson et al. 1973) indicates that there could well have been some lesser effect as early as 1954. Commencing in 1960 more adults tagged as Northwest smolts were captured in the Sevogle by anglers than ever before. None of them, however, were fish that had ascended, then fallen back through the counting fence. (Out of 742 fish tagged as wild smolts then angled as adults between 1961 and 1973, only three had first passed down through the fence at times of copper–zinc pollution. Two were later angled in the Northwest below the fence and one was angled in the main Southwest.) The Sevogle, about equal in flow to the Northwest at their confluence, is the most likely stream in which ascending adults could find haven from copper–zinc pollution coming down the Northwest.

The two principal effects of the copper–zinc pollution on adults can be compared in Fig. 5. The upper part illustrates correlation between fallback at the counting fence (May 16–October 15) and incidence of daily copper–zinc pollution reaching or exceeding 0.4 TU during the season ($r = 0.582$, $0.02 < P < 0.05$) from 1960 to 1973.

In 1960 and 1961 only intermittent measurements of copper–zinc pollution were made. From 1962

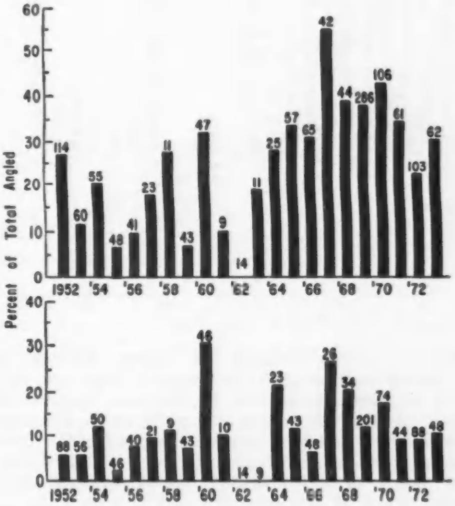


FIG. 4. *Upper* — Straying of Northwest Miramichi grilse and salmon, tagged as wild smolts, into other branches of the Miramichi system as shown by percentage of total anglers' catch in the home stream and elsewhere. Numbers above bars are total catch by anglers each year. *Lower* — Straying into the Sevogle River as percentage of total anglers' catch in the Northwest above and below the fence and in the Sevogle.

onward daily measurements were made from May to November. In Fig. 5, *Upper*, the scanty data for number of days of toxic units at or over 0.4 in these 2 yr have been replaced by the number of days showing fallback of grilse and salmon at the fence (solid line). If data for 1960 and 1961 are omitted on grounds of insufficient chemical analyses, the correlation is stronger ($r = 0.775$, $0.001 < P < 0.01$; broken line). Average prespawning fallback (to October 15) for the years 1960–70, i.e. before effective abatement measures were instituted, amounted to 7%.[1] The lower part of Fig. 5 shows correlation between straying into the Sevogle as measured by angling and incidence of pollution reaching or exceeding 0.4 TU during all but the last 2 wk (May 16–August 31) of the angling season ($r = 0.606$, $0.02 < P < 0.05$; solid line in Fig. 5, *Lower*). Again, data for incidence of pollution in 1960 and 1961 have been replaced by the number of days during the angling season which showed fallback. Catch data for 1962 and 1963 have been omitted from this analysis because few marked fish were available to anglers, reducing the reliability of estimates based on recovery of marks by angling (see section on EFFECT OF FISHING PRESSURE ON STOCKS for discussion of this matter). In both years pollution incidence was maximal (Table 3) and fallback substantial, hence data for these 2 yr seem to be inconsistent with respect to the other 12 yr.

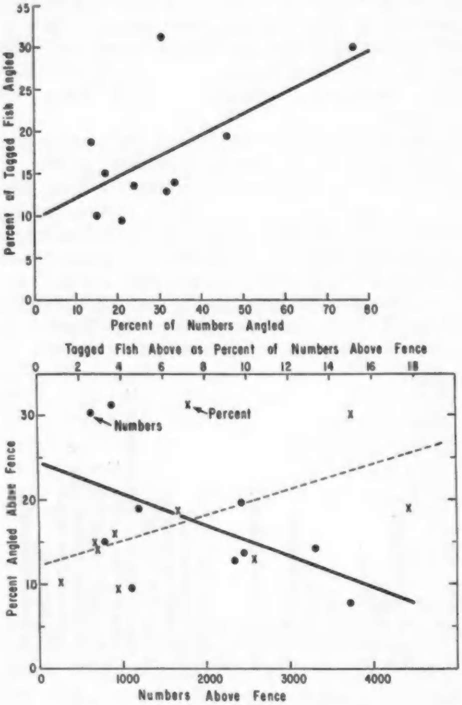


FIG. 5. *Upper* — Relation of salmon fallback at counting fence, measured as percent of total upstream run of grilse and salmon, to frequency (number of days per year) of copper–zinc pollution at the fence reaching or exceeding the avoidance level of 0.4 toxic units (1960–73). Solid line — $y = 2.60 + 0.10x$, SE y(est.) $= 4.10$; broken line — omitting 1960, 1961, $y = 1.33 + 0.09\times$, SE y(est.) $= 2.23$. *Lower* — Relation of straying into Sevogle to frequency of avoidance levels of copper–zinc pollution in the Northwest. Straying is measured as percent of smolt-tagged Northwest fish angled in the Northwest Miramichi above and below the fence and in the Sevogle (1960–73, omitting 1962, 1963 – see text). Solid line — $y = 10.18 + 0.29x$, SE y(est.) $= 5.96$; broken line — omitting 1960, 1961, $y = 11.62 + 0.19x$, SE y(est.) $= 5.84$.

A more conventional treatment of these data is to exclude 1960 and 1961 data on the basis of insufficient chemical analyses, and 1962 and 1963 data (also 1961) on the basis of insufficient angler catch of marked fish. Correlation between straying and fallback seems to be indicated but with a lesser degree of confidence ($r = 0.412$, $0.2 < P < 0.3$; broken line in Fig. 5, *Lower*). In my opinion, developed from field contact with this work, the associations indicated by the solid lines in Fig. 5 offer better descriptions of the salmon behavior observed, despite lack of rigid adherence to mathematical convention. Average straying into the Sevogle for the years 1960, 1961, and 1964–70 amounted to 17% as measured above.

As might be expected, there is some indication that the mining pollution detracted from angling above the counting fence ($r = -0.388$, $0.2 < P < 0.3$). But angling in the main stem, in contrast to the nonpolluted Sevogle, showed no increase ($0.7 < P < 0.8$).

Minimal average loss attributable to mining pollution between 1960 and 1970 is probably best estimated as the sum of the average take of tagged fish in the Sevogle (17%) plus the average prespawning fallback at the fence (7%) or about 25%. This loss was shared between all four stock components, i.e. early and late salmon and grilse.

---

[1] Elson et al. (1973) show fallback data averaging 9% for these 11 yr. A recheck of files indicates their data included normal descent of some overwintering kelts in spring and some spawned-out fish in autumn. The 7% excludes spring kelts and descents after October 15, which could have been spawned-out fish.

The formerly abundant late-run salmon (Fig. 2) suffered most, however, because of frequent parr-killing pollution (Table 3) on 20 to 25% of the river's rearing ground, this being about half of the area used by late-run fish.

Stock depletion from the mining operation through the 1960s is summarized: annual diversion of about 25% of the adult stock for all reaches of the river from the spawning grounds, removal of about 25% of the rearing ground from production, and reduction of late-run populations to levels from which they cannot recover normal abundance for several generations.

Damage probably indirectly associated with mining pollution occurred in several warm summers. Soon after heavy summer surges of copper–zinc pollution, a bacterial epidemic attacked salmon runs and other resident fish (Pippy and Hare 1969). Under such conditions fallback of adults with extensive skin lesions and growth of fungus was conspicuous.

PROCESSING FOREST PRODUCTS AND URBANIZATION

Industrial growth on the Miramichi has been even more dependent on exploitation of forest resources than on mining. In 1950 a mill to produce unbleached pulp was established on the Northwest branch of the estuary just above where it joins the larger Southwest branch (Fig. 1). Initially, production was about 110t (120 English tons)/day. This increased to over 180 (200) by 1961, 270 (300) by 1967, and 450 t (500 English tons) by 1969. Beginning in 1967 the process was gradually converted from production of unbleached kraft to over 80% bleached kraft in 1972. Until 1971 there was only primary treatment (removal of some solids) of the effluent. It was highly toxic to salmon parr in bioassays (Cook and Hoos 1971). In 1972 secondary treatment facilities were made operative, greatly ameliorating the local pollution situation (Côté 1973). Another company installed a mill, with much smaller capacity, to produce ground wood fiber on the opposite bank of the Southwest branch of the estuary (Fig. 1) in 1965. A plant for preserving wood structural materials discharged pentachlorophenol, creosote, etc. into the common estuary about 3.2 km (2 miles) below the kraft mill. Untreated urban sewage from the port towns of Newcastle (population 6500) and Chatham (population 7800) (Fig. 1) entered the estuary about 5 and 11 km (3 and 7 miles) below the kraft mill. Shipping to export the region's natural resources contributed oil spills and other forms of pollution. The deleterious effects of these pollutants on salmon behavior and survival are reviewed in Elson et al. 1973. By 1968, a year of comparatively low summer discharge, concern developed that pollution in the estuary might be delaying upstream migration of salmon. A study involving water movement in the estuary, pollution concentration, and salmon movements showed there was indeed delay and it was associated with pollution incident between the kraft mill and Chatham; diversion of migrating salmon from the Northwest arm into the Southwest arm was also indicated (Elson et al. 1972a).

As early as 1952 there was evidence, from recaptures of salmon marked as smolts in the Northwest, of some straying into the other branch, although in general there was a high degree of homing to the tributary of origin (Kerswill 1971). One simple measure of the amount of straying is the percentage of returning smolts taken by angling in the home stream and other tributaries. This is the scheme used above for measuring strays into the Sevogle consequent on mining pollution. Straying into the Main Southwest, measured in this way, shows an increasing trend since 1952 (Fig. 6, *Upper*). Lack

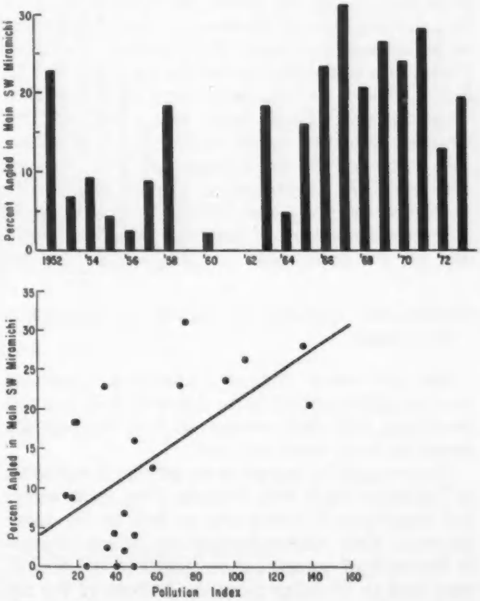


FIG. 6. Amount of straying of grilse and salmon tagged as wild seaward migrating smolts in the Northwest Miramichi River and recaptured by anglers in branches of the Mai Southwest Miramichi, expressed as percentages of yearly total angler catch of fish tagged as wild smolts. *Upper* — amount of straying each year. *Lower* — amount of straying in relation to daily production of a kraft mill on the Northwest arm of the estuary. Line is $y = 3.94 + 0.17x$, SE y(est.) $= 8.06$; $r = 0.597$, $P < 0.01$.

of straying for 1959 is puzzling, but for 1961 and 1962 few fish marked as wild smolts were available (see below). It is, in fact, correlated with increasing production of the kraft mill, using this as the best available index to increasing avoidance- causing pollution of the area (Sprague and Drury 1969). It cannot, however, reflect other things like excessive waste creosote and pentachlorophenol (both causing avoidance and/or death at very dilute concentrations) from the wood treatment plant, oil spills, etc. Logically high river discharge would dilute pollutants more than low discharge. Accordingly, the percent of angled, tagged fish of Northwest origin that diverted into the Main Southwest have been compared to a mill pollution index

$$= \frac{\text{mean daily production (English tons)} \times 100}{{}^{2}\text{mean water flow (cfs)}}$$

(1 English ton = 907 kg; 1 cfs = 0.028 m^3/sec). The resulting correlation ($r = 0.60$, $P < 0.01$) is illustrated in Fig. 6, *Lower*. It supports the idea that straying into the Southwest is partly dependent on pollution in the industrialized part of the estuary. (There was essentially no correlation ($r = -0.131$, $0.5 < P < 0.6$) between straying and water flow when the mill effluent factor was excluded.) This straying, measured by the angling catch of tagged fish amounted to an average of 21% between 1963 and 1971. It dropped to 13 and 19% in 1972 (a high-water year) and 1973 (a low-water year) following installation of secondary treatment facilities for the kraft mill.

COMMERCIAL CATCHES INCREASED BY ESTUARIAL POLLUTION

By 1967 some commercial salmon fishermen were complaining that heavy estuarial pollution was interfering with their success. In fact, the opposite seems to have been the case.

Those operating setnets in the estuary complained of fouling of their nets by pulp fiber, bark waste, and sometimes oily deposits as well as the usual seaweed. They also remarked on recent changes in behavior of salmon; those gilled in net leaders were said to be taken from the bottom of the net (where the water is more saline) rather than in the fresher surface waters as formerly. Hydrographic patterns which show cleaner inflowing salt water at the bottom and polluted fresher water at the surface are illustrated in Elson et al. 1972a. The same paper comments on the large amount of to-and-fro movement shown by salmon within the polluted section. Later unpublished studies (Dr A. B. Stasko personal communication) indicated a reluctance on the part of salmon placed in the cleaner downriver part of the estuary to enter the more heavily polluted zone upriver.

Fishermen operating driftnets from near the mouth of Miramichi Bay (Fig. 1) to over 30 km (20 miles) off also commented on apparent relation between pollution of the estuary and changed behavior of salmon in the offing of the bay. They said the fish appeared to mill about in the offing and earlier patterns of waves of fish being taken by the drifters, then passing progressively inward through the estuary, were much less evident. Drifters complained, too, of periodic oil slicks fouling their nets. They said the salmon would not approach an oil-fouled net and the fishermen normally avoided even pumping out bilge water from their boats while their nets were set.

A comparison of catches in two segments of the Miramichi fishery (Fig. 1 and 7) shows that changes in the pattern of relationships between fishermen and salmon did occur, beginning about 1960. Average annual landings for the period 1950–59 were 88 t (194,500 lb) mostly by driftnets and 49 t (108,000 lb) all by trapnets and six to nine fixed gillnets. Synthetic nets were introduced to the driftnet fishery between 1959 and 1961. The more efficient (e.g. Hewson 1951) polyfilament nylon nets may have increased their chance to take approaching fish first. But more than this seems to have been involved.

The recent course of the commercial fishery is illustrated in Fig. 7, *Upper*. In this figure landings for each segment of the fishery, the outer fishery (100–120 driftnets and about 40 setnet berths), and the inner fishery (180–220 berths) are shown as percentages of the means for each segment from 1950–59. This period was selected as one in which the fishery seemed not to abstract unduly from stocks. Stocks are believed to have been capable of self-perpetuation under conditions then pertaining.

An analysis of relations between the outer and inner fisheries is illustrated in the lower part of Fig. 7. About the time (1959–61) of conversion of the driftnet fishery from hemp to nylon netting, this outer fishery took a relatively larger share of total landings. As kraft mill production and conse-

---

[2] Water flow data (Water Survey of Canada) for the Little Southwest Miramichi (for the months of July and August only) were used because they are the only data for the entire period of interest: this river is intermediate in position between the Northwest and Main Southwest (correlation of flows of Little Southwest with Northwest (1962–72) $r = 0.94$, $P < 0.001$; Main Southwest (1961–72) $r = 0.90$, $P < 0.001$).

quent pollution increased in the mid 1960s, the discrepancy increased to a maximum in 1967 — also a year of maximum diversion of Northwest fish into the Main Southwest. This was also a year of increasing production by the kraft mill, of low water flow, and therefore probably of maximum delay and diversion of salmon in the estuary (see Fig. 6, *Upper*). Despite the change in pattern of the fisheries, total landings were high in the 8 yr, 1964–71 (driftnets averaged 194 t (426,800 lb); setnets 38 t (83,900 lb)). The total catches, representing about 70% increase over the 1950–59 level, were taken in the face of decreasing stocks in the Northwest (Fig. 2, early and late salmon) and the rest of the system (Ruggles and Turner 1973).

Distant salmon fisheries, which might be considered to be a part of the growing industrial complex, also increased their effort, hence exploitation of salmon, including those of Miramichi origin during the 1960s (Elson 1973b; Turner 1972). They contrast with Miramichi home water fisheries which have been pegged at a constant level for several decades. Chung's (1973) data show increases in salmon fishermen (53%) and landings (from 1400 to 1768 t (3.1–3.9 million lb) = 26%) in Newfoundland between 1961 and 1970. In the same period (ICNAF 1973) the new West Greenland fishery increased from about 127 to 2146 t (280,000–4.7 million lb) or by 16 times. Evidence that the West Greenland fishery does abstract from Miramichi stocks enough to noticeably decrease escapement and recruitment is presented by Paloheimo and Elson (1973).

Both home and distant fisheries have thus contributed to the decline in Northwest Miramichi large salmon stocks shown in Fig. 2.

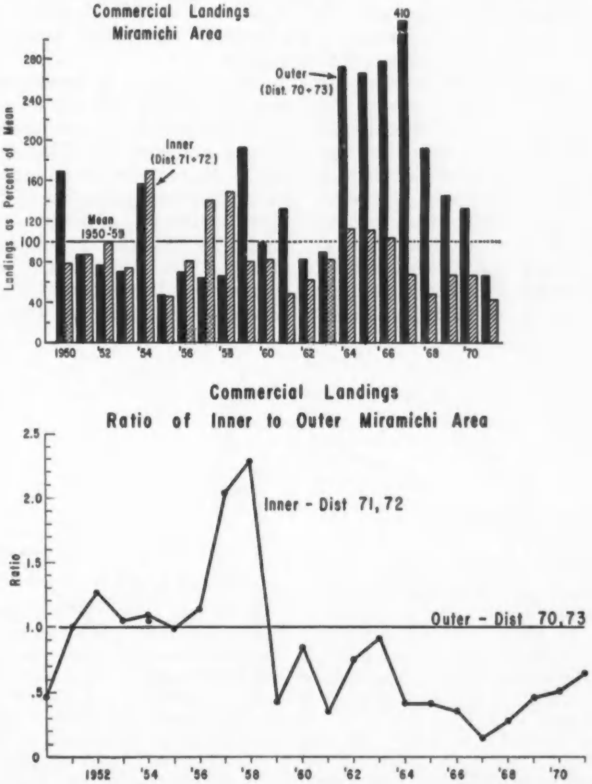


FIG. 7. *Upper* — Commercial landings of Atlantic salmon in the inner and outer Miramichi fisheries shown as percentages of mean landings of each fishery for 1950–59. The fisheries were banned in 1972. *Lower* — Changing ratio of inner to outer segments.

EFFECT OF FISHING PRESSURE ON STOCKS

Industrialization and economic growth have meant increasing demand for the sport of salmon angling. This demand is sometimes measured by the number of rod days spent angling. (In the present context 1 rod day = one angler fishing for any part or all of 1 calendar day.) Most Maritime salmon rivers are fairly well saturated with anglers so that here rod days are more a measure of the capacity of rivers to supply the commodity. As Chung's (1973) data show, there was not much change in the long-established angling effort applied in New Brunswick between 1953 and 1970 (mean, 78,562 ± 12,676 or 16% [SD] rod days per year). But in Newfoundland effort increased by 2.7 times between 1957 (33,776 rod days) and 1970 (90,321 rod days), with increasing demand being met by increased road accessibility of streams.

In areas like the Miramichi this demand has resulted in only moderate change in pressure in spite of the dwindling stocks of recent years. There is some tendency for abundant fish in the river to attract good angling (Fig. 8, *Left* — $r = 0.536$, $0.1 < P < 0.2$). However, a year of good fishing is likely to be followed by heavy effort the next year whether or not stocks fall off. Change in demand lags behind decreasing stocks. But there is less lag in demand when stocks improve after a low period. Anglers flock to good fishing with much less delay than they desert poor fishing, and both anglers and outfitters are quick to publicize good fishing. Correlation ($r = 0.794$, $0.001 < P < 0.01$) between total rod days applied on the Northwest Miramichi above and below the fence and catches, as indicated by Canadian Fisheries Service records for 1964–73, is illustrated in Fig. 8, *Right*. Increased fishing pressure has meant increased catches and therefore greater removal from potential spawning stocks.

The accuracy of creel census methods is sometimes questioned. The salmon creel census data provided by the Fisheries Service admittedly tend to express minimal estimates of catch. For the Northwest above the counting fence, two estimates of catch by anglers are available. One is from known numbers of fish passed above the fence and the usual creel census (available separately only since 1964), the other is from known numbers of tagged grilse and salmon liberated above the fence and numbers of tagged fish reported in anglers' catches from above. There is moderately good correlation ($r = 0.632$, $0.02 < P < 0.05$) between the two methods of estimating exploitation rates by anglers (Fig. 9, *Upper*).

The tag system, of course, involves the assumption that tagged fish will be distributed the same, act the same, and be removed in the same proportion as untagged fish. This assumption might be met if the populations of tagged fish were a more or less constant proportion of the untagged populations each year, i.e. a nearly constant dilution of tagged by untagged populations. But with many untagged fish present there are relatively fewer chances of taking a tagged fish and assumption of common catchability between the two kinds is

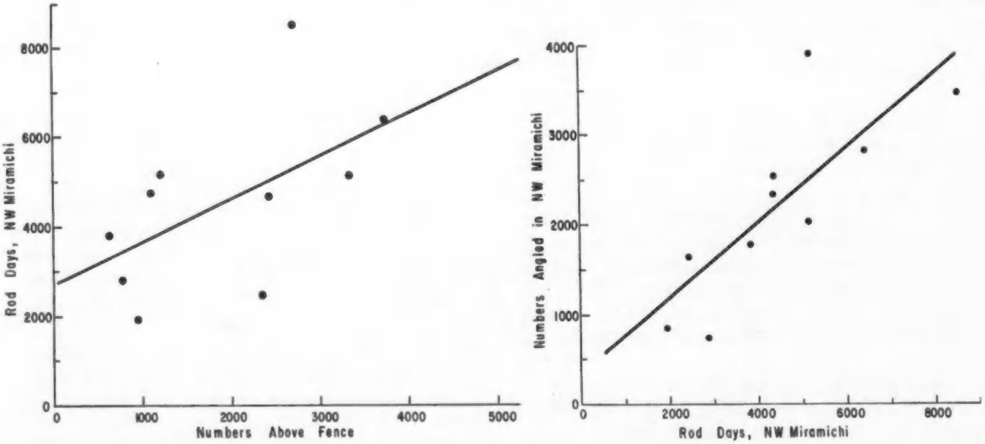


FIG. 8. *Left* — Dependence of angler effort (= rod days) applied on abundance of grilse and salmon in a river. The line is $y = 2708 + 0.95\times$, SE y(est.) = 1570; $r = 0.536$, $0.1 < P < 0.2$. *Right* — Dependence of catch on angler effort. The line is $y = 338.34 + 0.42\times$, SE y(est.) = 592; $r = 0.794$, $0.001 < P < 0.01$.

weakened. This is illustrated in Fig. 9, *Lower*. The black dots and solid line indicate ($r = -0.558$, $0.05 < P < 0.10$) that with many fish, mostly untagged, above the fence, anglers took lesser percentages of the tagged fish. (A similar but weaker negative correlation occurs when percentage of tagged fish angled is compared to rod days applied above the fence ($r = -0.471$, $0.1 < P < 0.2$)). However, when the same data are rearranged to show the catch from tagged fish available above the fence (*x*'s and broken line), positive correlation ($r = 0.547$, $0.1 < P < 0.2$), though with a lesser degree of confidence, is restored. This again points to the importance, when possible, of knowing the mixture of tagged and untagged fish when the object is to estimate populations and spawning escapement.

Learning this mixture is not always feasible, however. In Fig. 10, *Upper*, are shown year-by-year estimates of angler exploitation of grilse and salmon above the counting fence from 1964 to 1973. The left side of this diagram features the estimates derived from tagged fish put up and those subse-

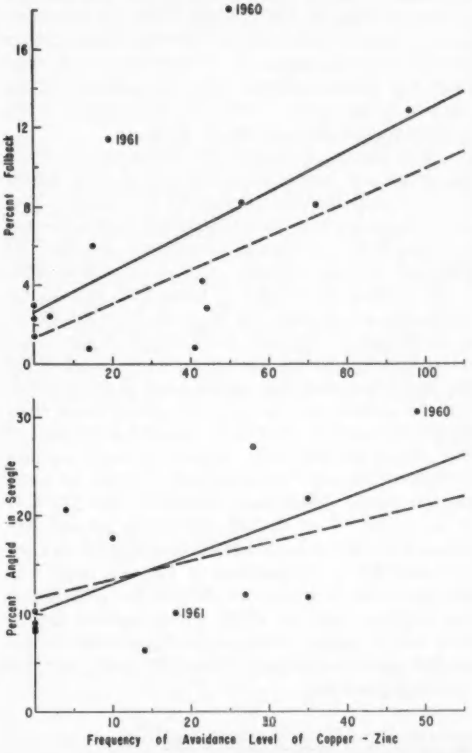


FIG. 9. *Upper* — Correlation between percent of population above fence taken by angling, as measured by percent angler recapture of tagged fish (wild smolts only) and by counts at fence and creel census. The line is $y = 9.61 + 0.25x$, SE y(est.) $= 5.6$; $r = 0.632$, $0.02 < P < 0.05$. *Lower* — Solid line, dependence of percent angler recapture of tagged fish on abundance of fish, mostly untagged, in the river. The line is $y = 24.74 - 0.00376\times$, SE y(est.) $= 5.7$; $r = -0.558$, $0.05 < P < 0.10$); broken line, dependence of percent angler recapture of tagged fish on proportion of tagged fish in the population. The line is $y = 12.19 + 0.74x$, SE y(est.) $= 6.0$; $r = 0.547$, $0.1 < P < 0.2$.

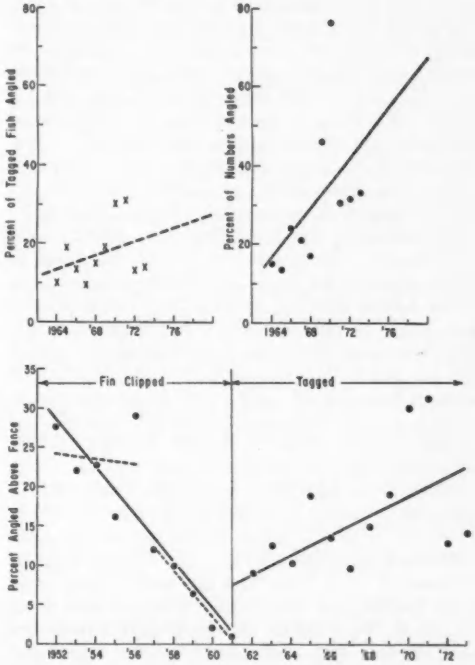


FIG. 10. *Upper* — Recent upward trend in angling exploitation as shown by two methods. *Left*, percentage of tagged fish above the fence taken by anglers. The line is $y = 16.99 + 0.89x$, SE y(est.) $= 6.75$; $r = 0.354$, $0.3 < P < 0.4$. *Right*, percentage of number of fish released above fence taken by anglers. The line is $y = 29.16 + 3.17x$, SE y(est.) $= 15.46$; $r = 0.508$, $0.1 < P < 0.2$. *Lower* — Trends in angling exploitation for 1952–61 and 1961–73. *Left*, solid line, $y = 31.38 - 2.99x$, SE y(est.) $= 4.33$; $r = -0.893$, $P < 0.001$, is a composite of broken lines — for 1952–56, no trend ($0.8 < P < 0.9$) and for 1957–61, $y = 15.42 - 3.02x$, SE y(est.) $= 0.72$; $r = -0.986$, $0.001 < P < 0.01$. *Right*, line is $y = 6.15 + 1.28x$, SE y(est.) $= 6.31$; $r = 0.606$, $0.02 < P < 0.05$.

quently caught for the same years. Any trend shown towards taking a higher proportion of fish with passing years is nebulous ($r = 0.354$, $0.3 < P < 0.4$) at best. The right side shows the estimates derived from counting fence and catch records, including both tagged and untagged fish. A rising trend is indicated with more confidence ($r = 0.508$, $0.1 < P < 0.2$) than by the tag system (although the two slopes are not identifiably different ($0.2 < P < 0.3$)). It is sufficiently steep to give some cause for concern about future recruitment if salmon populations are low.

Trends from 1952–73 in exploitation by angling above the fence are shown in Fig. 10, *Lower*. Data for 1952–61 are based on finclipped fish above the fence, 1965–73 on tagged fish, and 1961–64 on both finclipped and tagged fish. Different trends are indicated for the first 10 yr and the last 12. From 1952–61 these data indicate a strong downward trend in exploitation by angling ($r = -0.893$, $P < 0.001$). When recaptures were checked against mixture of marks in the population, i.e. total fish available and total marked fish available, no correlations indicating the trend to be an artifact were evident. At first glance this downward trend is startling. However, it is established to a large extent by data from 1957–61. In 1956 stocks were reduced as a result of DDT spraying in 1954 and were low for three successive years, improved in 1959 (when marked fish constituted only 3% of the population; average for 1957–61, 10%) and dropped again in 1960 (see Fig. 2, early run). This may have affected angler response to the river. The variable mixture of marked fish (i.e. dilution factor) may also have contributed to unrealistic assessment. From 1961–73 an upward trend ($r = 0.606$, $0.02 < P < 0.05$) in catch by anglers is indicated by tag return data. Difference between this and the earlier trend is obvious ($P < 0.001$). Tags are more conspicuous than finclips and may bring better returns from fishermen. The trend for the second period conforms well enough with that shown by the right-hand side of Fig. 10, *Upper*. Although the slope is not as steep in the lower figure, any difference between the two could be a result ($0.2 < P < 0.3$) of the variability inherent in each line.

Tag returns from fish tagged as native smolts and caught by anglers above the fence (1964–73) indicate that 15% of the tagged grilse and 18% of the tagged large salmon liberated above the fence were caught. But creel census and fence counts indicate that 39% of all grilse and 52% of all large salmon passing up by the end of August were caught. Average annual exploitation of total populations was 18% as measured by tag returns and 31% as measured by creel census and fence counts. Thus a correction factor of 72% would have to be added to the exploitation rate measured by tag returns to give the same rate as that measured by creel census and fence counts.

Recapture of tagged fish from a known tagged population sometimes gives a less reliable estimate of exploitation than creel census. This seems to be the case particularly when there are not uniform mixtures of tagged and untagged fish in the populations under study. The counting-fence-and-creel-census system probably gives a more dependable estimate of angler exploitation than tags alone but counting fences or equivalent methodology are not always feasible on large rivers. Both systems have their place and one can reinforce the information gained from the other. In the present study, data from the counting fence and creel census will be used to estimate the impact of angler exploitation on spawning density above the fence.

Large salmon, as opposed to grilse, are the most important for recruitment (Paloheimo and Elson 1973). It will therefore be useful to examine how recruitment patterns have responded to the changes in ecological conditions, including commercial fisheries, estuarial pollution, and angler exploitation.

For studies of Northwest Miramichi salmon recruitment, a basic tool has been the counting fence. It is subject to periodic malfunction during high water and to late installation or early removal for the same reasons, plus heavy icing in November. But the counts are believed to include more than 80% of actual runs and to be a useful indication of the magnitude of runs. Counts of large salmon correlate well with total anglers' catches of large salmon in the Northwest, shown in Fig. 11, *Left* ($r = 0.700$, $P < 0.001$). Changing relationship between counts of large salmon and anglers' catches of those fish are illustrated in Fig. 11, *Right*. In this figure mean values for 1950–59 for both count and anglers' catch = 100%, giving a ratio of 1:1. This was a period when populations could be regarded as self-sustaining. Values for each year are then expressed as:

$$\frac{\text{count as \% of 1950--59 mean count}}{\text{catch as \% of 1950--59 mean catch}} = \frac{\text{(count)(1950--59 mean catch)}}{\text{(catch)(1950--59 mean count)}}$$

The change, in 1964, from fence counts being higher than angling take (average ratio 1.35:1.00) to lower (average ratio 0.39:1.00) reflects sustained angling pressure on smaller numbers of fish (yearly average at fence, before 1964, 742; after, 151). Much of this was attributable to increased angling below the fence, because those angled above are also included in fence counts.

Reduced runs of large salmon at the fence are attributable not only to anglers below but also to effects of the commercial fishery, its catch being increased by pollution in the upper estuary, much of it emanating from the kraft mill on the Northwest arm. The increasing proportion of this catch is illustrated in Fig. 12, *Upper*, using the same system as in Fig. 11, *Right*. For Fig. 12, *Upper*, the 1950–59 means for counts of salmon at the fence and for commercial landings each equals 100% and all values are recalculated as

$$\frac{\text{(count)(1950–59 mean landing)}}{\text{(landings)(1950–59 mean count)}}$$

The figure illustrates that the drift fishery, beginning in the late 1950s, took an increasing portion of the total stock (perhaps associated first with introduction of nylon nets and later with excessive pollution of the estuary); then that the inner setnet fishery, beginning about 1962, took an increasing proportion (probably associated with pollution in the estuary). For the period 1964–71 the ratio for the fence counts to total landings, calculated as above, had dropped from 1:1 in 1950–59 to 0.09:1.

Fig. 12, *Lower*, illustrates a similar comparative treatment of data for the commercial fishery and angling of large salmon in the three quarters of the Miramichi basin lying within Northumberland County (Fig. 1): about three quarters of all angling on the system is done here. The Main Southwest Miramichi enters the Southwest arm of the estuary and was thus comparatively free from pollution by kraft mill effluent and other sources entering on the Northwest side. Although the commercial fishery took an increasing share from 1959 or 1960 on, for the 1964–71 period the earlier 1:1 ratio for this part of the system dropped only to 0.21:1 in the latter period.

Is there any basis for comparing river populations measured by fence counts on the one hand and angling on the other? Angling catches in the main stem of the Northwest Miramichi above and below the fence can be compared to those for the entire Miramichi system (data for Northumberland County only). Correlation ($r = 0.518$, $0.01 < P < 0.02$) of numbers of large salmon taken by both fisheries gives confidence in the validity of the comparison. So, too, does correlation ($r = 0.427$, $0.02 < P < 0.05$) of numbers of large salmon ascending to the fence with numbers taken in the total angling fishery (Northumberland County). Again using the same method of analysis as for Fig. 7, 11, and 12, Northwest angling catches and counting-fence runs of large salmon are compared to angling catches of the same group in the entire system in Fig. 13. After 1963 the ratio of fish reaching the counting fence fell off relative to angling in the Northwest (Fig. 11) and to angling in the total

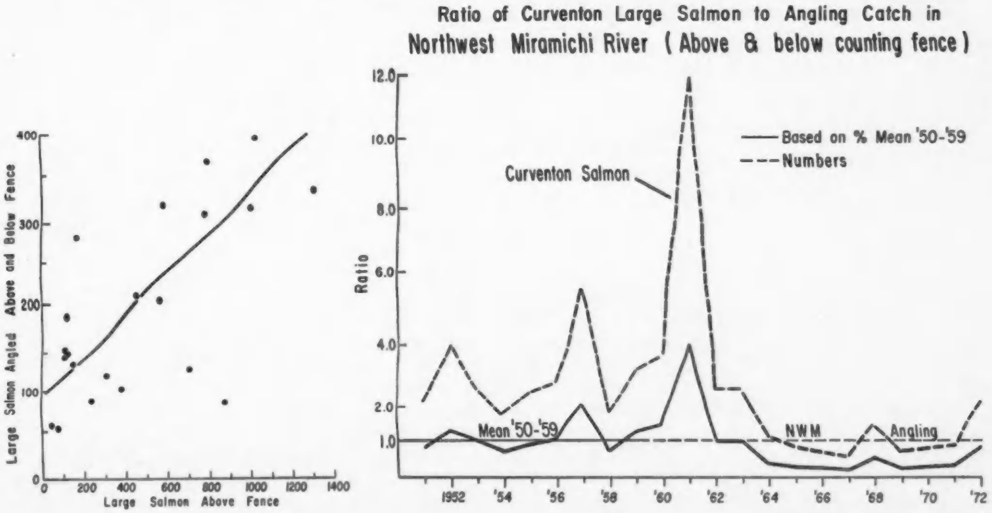


FIG. 11. *Left* — Correlation between total numbers of large salmon taken by anglers in the Northwest and numbers of large salmon ascending to fence. The line is $y = 94.14 + 0.24x$, SE y(est.) $= 94.18$; $r = 0.700$, $P < 0.001$. *Right* — Changing ratios of large salmon reaching fence to catch by anglers; broken line calculated from actual numbers, solid line from percentages of means for 1950–59 (for which ratio = 1).

system (Fig. 13). This again indicates substantially increased angling pressure below the fence. Nevertheless, the two correlation coefficients above support the validity of drawing comparisons between Northwest river populations measured at the counting fence and total Miramichi system populations measured by angling.

Pollution of the upper estuary enhanced the commercial salmon fishery by delaying upward passage into fresh water. This acted more strongly on fish of Northwest than those of Main Southwest origin (Elson et al. 1972a).

Increased angling pressure in the Northwest below the counting fence removed a much greater proportion of large salmon entering the river after 1964 than before. Moreover, at least from 1964 onward there has been a trend for increasing exploitation of river stocks by angling above as well as below the counting fence (Fig. 10, *Upper right*).

SPAWNING RECRUITMENT AND THE BALANCE OF STOCKS

The salmon stock of the Northwest Miramichi should not be regarded as a single homogenous stock. There appear to be four important segments: early-run 2-sea-winter salmon and 1-sea-winter grilse using the upper reaches of the river for spawning and rearing and late-run salmon and grilse using the lower reaches. It has also been shown how the total adult stock and each segment thereof have suffered periods of drastic decline. Through the 1960s large salmon, particularly, fell to critically low levels in terms of reproductive potential. The large salmon segments have been shown (Paloheimo and Elson 1973) to contribute disproportionately heavily to reproduction as compared to grilse. This is partly because of more favorable sex ratios (half or more of Northwest large salmon but only one third of grilse are females) and partly because of the greater fecundity of larger fish. The young of both grilse and salmon have been hit equally by environmental debasement of the river. Grilse can, but don't always, get through the 14-cm (5 1/2 inches) stretched mesh trapnets of the inner home fishery. Hence the large salmon have been depressed far more than grilse by the combined operations of pollution and increasingly extensive and effective distant and home commercial fisheries.

Recruitment needs for maintenance of Atlantic salmon stocks were suggested by Elson (1957a, 1962c). The values given referred to potential egg deposition, meaning the number of eggs brought into a river by adult females, assuming a sufficiency of males for breeding and assuming also that some of both sexes would be removed by anglers, poachers, and other forms of mortality before spawning. The values suggested were based on observation of adults and young in several rivers. (In the text below, English units were used in computing population densities for eggs and young as well as fecundity. To convert to metric system, 100 yd^2 = 83.6 m^2 and no./100 m^2 = no./100 yd^2 × 1.2; 1 lb = 0.454 kg and no. of eggs/kg = no./lb × 2.2.)

Eggs should be brought into the river at an average rate of 200/100 yd^2 (240/100 m^2) for the entire stream (not just for spawning beds, where density would be much greater). This was enough to saturate the smolt-producing capacity of most Canadian Atlantic salmon rivers (Elson 1962b). Potential egg deposition at the rate of 300 eggs/100 yd^2 (360/100 m^2) was not followed by any noticeable increase in underyearlings the next year compared to a rate of 200 (240/100 m^2). This rate assumed the rivers to be in a nearly natural state with no drastic environmental debasement. It also assumed fishing pressure, both commercial and recreational, at the more or less constant levels pertaining in the 1950s.

Neither assumptions of normal environmental constancy nor of constant fishing pressure are valid in the 1970s. Public environmental consciousness and governmental pressure for pollution abatement and environmental protection will, hopefully, mean that rearing areas will remain about as suitable as two decades ago (except, of course, where hydroelectric power dams have flooded rearing areas). But fishing pressures have changed and can be expected to continue changing. This upward trend in angling should be expected to continue unless Management dictates otherwise. The West Greenland high seas fishery will be phased out in 1976 (ICNAF 1972), but the Greenland inshore fishery will continue. The ban imposed on New Brunswick commercial fisheries in 1972 may or may not be lifted or modified by 1977 or later.

A more sensitive index for spawning density than is provided by potential egg deposition (index$_{pe}$) is needed. Data available now which were not available 10 yr ago permit developing values for virtual egg deposition (index$_{ve}$). Virtual egg deposition is used here to indicate estimates of egg deposition which take into account known removals of salmon and grilse which had already entered the river (and yielding potential egg deposition) by angling, poaching, premature descent, or other loss to spawning potential.

Table 4 gives estimates of virtual egg deposition as developed for that part of the Northwest Miramichi above the counting fence from 1950–73. These estimates are considerably closer to real values than those of potential egg deposition used by Elson in 1957a and 1962c. They are also better approaches to the real situation than those used in Elson

(1973b) because they consider loss by premature descent as well as angling. Estimates of loss by angling for the period 1950–63 are subject to weakness (Elson 1973b), i.e. separate creel census data above the fence are not available and a general assumption is made of 9% loss of salmon and 20% of grilse to anglers, from Kerswill's (1971) data. Separate creel census data are available from 1964 on. As noted earlier, loss by premature descent does not include any spring descent of kelts which may have overwintered in the river; neither does it include any descent after October 15, considered as spawned-out fish. Bases for estimating fecundity have been improved. An earlier estimate of 10-lb (4.5-kg) average weight for female salmon is replaced by one of 8 lb (3.6 kg), derived from weights of salmon tagged as Northwest smolts, then subsequently recaptured in the estuarial fishery (234 fish), at the counting fence (37), or taken by angling (49). Allowance was made for a 0.5-lb (0.23-kg) loss of weight between estuary and spawning as indicated by average weights of the large salmon taken in estuary and fresh water. Average weight of 416 grilse taken at the fence was 3 lb (1.4 kg). Fecundity

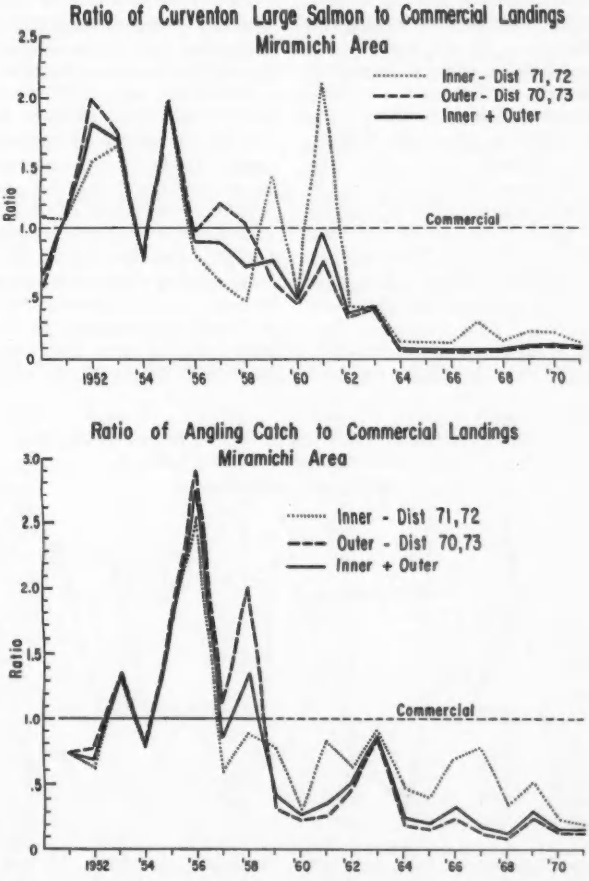


FIG. 12. *Upper* — Changing ratios in numbers of large salmon reaching the counting fence to landings in the Miramichi commercial fishery (each mean for 1950–59 = 100%). *Lower* — Changing ratios in numbers of large salmon taken by anglers in the entire Miramichi system within Northumberland County, to commercial landings (each mean for 1950–59 = 100%).

of females is calculated by assuming 800 eggs/lb (1764/kg) of live weight. This value was found to pertain to Pollett River grilse (Elson 1957a), to fall within the range given by Baum and Meister (1971) for 8-lb (3.6-kg) Maine salmon, and is closely approximated by the average of 730 eggs/lb (1606 eggs/kg) for five Northwest Miramichi salmon taken in October 1973.

For purposes of generalization, expression as total egg deposition in a particular river is less useful than expression as a rate or density. Numbers/100 yd^2 = index is convenient and has been used before (multiply English system indices by 1.2 to convert to metric indices). Index$_{ve}$ is used below for virtual egg deposition and index$_{pe}$ for potential egg deposition.

Using the new data for fish weight and fecundity, the older required index$_{pe}$ of 200 (metric = 240) (Elson 1957a) should be revised downward to index$_{pe}$ = 160 (192). This was the average for 1950–59 when populations still appeared self-perpetuating. The equivalent index$_{ve}$, from data in Table 4, is 136 (163) which might for a margin of safety be rounded off to index$_{ve}$ = 140 (168). With similar rounding, this was composed of a contribution from salmon, index$_{sve}$ = 85 (102) and from grilse, index$_{gve}$ = 55 (66), i.e. about 60% from salmon and 40% from grilse.

During the next 12 yr, with increasing exploitation of large salmon and other problems for both salmon and grilse, egg contributions, by 1971, dropped to index$_{sve}$ = 3 (4) and index$_{gve}$ = 16 (19). The salmon contribution was thus reduced to only 16% of total egg deposition which, at index$_{ve}$ = 19 (23) was only 14% of the required amount.

The 1972 ban on home commercial fishing did result in noticeable improvement, bringing average spawning (1972, 1973) up to about index$_{ve}$ = 75 (90) or nearly 55% of the desirable amount. Index$_{gve}$ at about 50 (60) is considered to presage good production of grilse by 1976 or 1977. But index$_{sve}$ at about 24 (29) is still less than one third of the desirable amount and full recovery of large salmon stocks seems unlikely to occur until about 1982. Only by then are the progeny of fish spawned in 1972 likely to return in sufficient numbers to restore the original balance of stocks.

Values for egg deposition given above indicate the respective contributions by salmon and grilse, but not by early- and late-run divisions of each group. Available data have not yet been examined to see whether it may be possible to estimate the relative contributions of each of these four segments of the overall Northwest salmon population.

Population densities of the young in upper vs. lower reaches shed some light on young recruitment to early vs. late stocks. This is because early-run fish tend to reproduce in the upper reaches and late-run in the lower. Data from annual late summer assessment of young, by electrofishing, are given

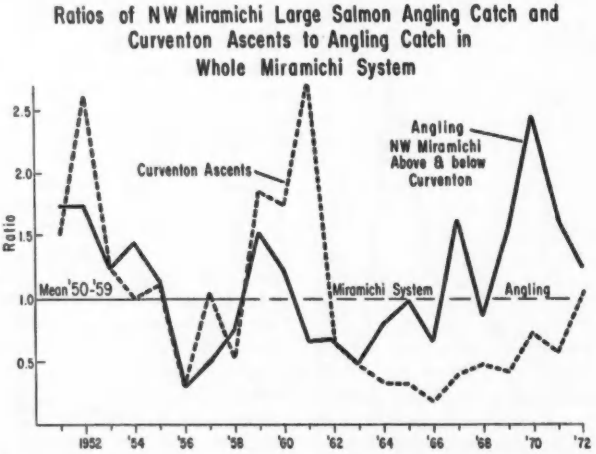


FIG. 13. Ratios for numbers of large salmon angled (solid line) in the Northwest Miramichi and for numbers reaching fence (broken line), to numbers angled in the Miramichi system (Northumberland Co. only). Counting fence numbers expressed as percent of their mean for 1950–59, Northwest and Miramichi system angling as percent of means for 1951–59 (ratios for the means = 1).

as English indices (no./100 yd^2) in Fig. 14. In this figure the distinction between small and large parr is one of size, not age. Large parr are those over 10 cm in total length (tip of nose to tip of tail). They are likely to metamorphose (Hoar 1939) to smolts the following spring (Elson 1957b). Throughout most of the period illustrated in Fig. 14, small parr are mostly yearlings and large parr 2-yr-olds. But the proportions are somewhat variable depending on good or bad years for growth (e.g. Elson and Kerswill 1966), location in the river (which relates to temperature), and possibly other factors. The small parr group, being an accumulation of 1+ and 2+ fish, sometimes outnumbers the underyearlings. Conspicuous examples in the figure are the underyearlings of 1955 and 1968 which contributed small parr to 1956 and 1957 populations and to 1969 and 1970 populations. Moreover, between 1967 and 1972 there was a shift, as already mentioned, from predominantly 3-yr smolt age to predominantly 2-yr. Late summer small parr should not be evident as such in a stream giving entirely 2-yr smolts, e.g. the Pollett (Elson 1962b).

The grey bands in Fig. 14 indicate desirable population levels for each group (Elson 1967).

Figure 14 indicates that early-run fish populations have been maintained moderately well even since 1959. But reference to Table 4 indicates that after 1960 and until 1973 this was dependent to a large and increasing extent on contributions from grilse.

In the lower reaches occupied by late-run fish, many of the small parr are comparatively large and apparently do change to smolts the following spring. But after the first year of heavy copper–zinc pollution few parr of either size-group were evident. Even the abundant late grilse run of 1963 (Fig. 2) was followed by comparatively few lower reach underyearlings in 1964 or parr in 1965 and 1966. Young of late-run stock remained at extremely low, almost negligible levels through 1972. There is, however,

TABLE 4. Estimates of virtual egg deposition in the Northwest Miramichi River above the counting fence at Curventon, 7 miles (11 km) above head of tide. Salmon (2-sea-winter and older) — calculated as 50% females and average weight 8 lb (3.6 kg); grilse (1-sea-winter) — as 33% females and average weight 3 lb (1.4 kg); fecundity — as 800 eggs per lb (1764 per kg) live weight of females; total river area accessible to spawners estimated as 3 × 10^6 yd^2 (2.5 × 10^6 m^2) or nearly 70 miles (113 km) and about 25 yd (23 m) average width. (No./100 m^2 = no./100 yd^2 × 1.2).

	Spawning escapement		Eggs deposited × 10^6			Index = no./100 yd^2			% of eggs by	
Year	Salmon	Grilse	Salmon	Grilse	Total	Salmon	Grilse	Total	Salmon	Grilse
1950	661	1540	2.115	1.232	3.347	71	41	112	63	37
1	728	1798	2.330	1.438	3.768	78	48	126	62	38
2	1190	1709	3.808	1.367	5.175	128	45	173	74	26
3	903	1720	2.890	1.376	4.226	97	45	142	68	32
4	981	2039	3.139	1.631	4.770	105	54	159	66	34
5	702	2135	2.246	1.708	3.954	75	57	132	57	43
6	506	603	1.619	0.482	2.102	54	16	70	77	23
7	639	664	2.045	0.531	2.576	68	18	86	79	21
8	520	1864	1.664	1.491	3.155	56	49	105	53	47
9	907	5827	2.902	4.662	7.564	96	156	252	38	62
1960	331	1663	1.059	1.330	2.390	35	45	80	44	56
1	650	702	2.080	0.562	2.642	70	18	88	79	21
2	196	1629	0.627	1.303	1.930	20	44	64	32	68
3	244	4064	0.781	3.251	4.032	25	109	134	19	81
4	91	4355	0.291	3.484	3.775	10	116	126	8	92
5	105	1313	0.336	1.050	1.386	11	35	46	24	76
6	78	2200	0.211	1.760	1.971	7	59	66	11	89
7	126	1834	0.403	1.107	1.510	14	36	50	27	73
8	63	781	0.202	0.625	0.826	7	21	28	24	76
9	60	1189	0.192	0.951	1.143	6	32	38	17	83
1970	58	89	0.186	0.071	0.257	6	3	9	72	28
1	32	583	0.102	0.466	0.569	3	16	19	18	82
2	334	1489	1.069	1.191	2.260	35	40	75	47	53
3	117	2266	0.374	1.813	2.187	12	61	73	17	83

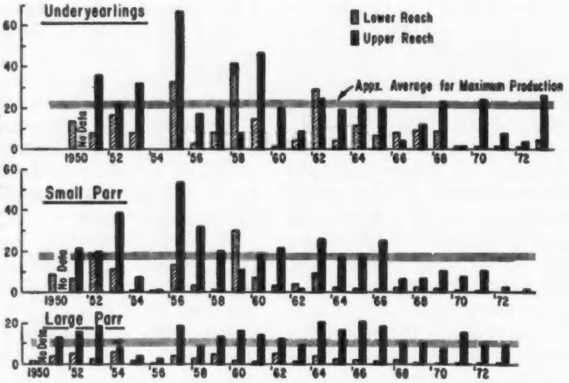


FIG. 14. Average abundance of young salmon, found by systematic electrofishing in the same sample areas of the Northwest Miramichi each year.

evidence of minor recovery of late-run underyearlings in 1973.

GENERAL CONSIDERATIONS AND PREDICTIONS

An analysis of what has happened to Northwest Miramichi salmon has only academic interest unless it can contribute to future management of the Atlantic salmon resource of this and other rivers.

Chemical debasement of rearing environment by spraying DDT to preserve the forest resource was recognized early. Mitigating changes in spraying procedure (Flieger 1964) and in the chemicals, from lethally toxic and persistent chlorinated hydrocarbons to less dangerous (for fish and aquatic insects) organophosphates followed within 10 yr. These changes arose, at least in part, from close cooperation between people interested in the forest resource (gross annual value to New Brunswick over $200 million) and those interested in anadromous fisheries (gross annual value to New Brunswick, in excess of $10 million (A. L. W. Tuomi, Recreational Fisheries Branch, Department of the Environment, Ottawa, personal communication). These changes probably meant more to conservation of salmon in many other streams than to those of the Northwest Miramichi which received DDT only in 1954, 1956, 1957, and 1964

Chemical debasement of salmon breeding environments from mining was first recognized as a threat to stocks in the Northwest Miramichi in 1960. This recognition was followed not only by continued research into the various facets of the impact of such pollution on Northwest salmon, but by a much more extensive Federal–Provincial Northeastern New Brunswick Mine Water Quality Program (Montreal Engineering 1972) which has led towards mitigating pollution abatement on this and other affected streams.

The deleterious effects of pulpmill waste effluent in rivers were recognized quite a few years before study of the impact of such pollution on behavior of Miramichi salmon was begun in 1969. There appeared to be widespread acceptance that once such pollution had reached tidal waters it was rapidly diluted to become comparatively innocuous. That such pollution might adversely affect migratory behavior of fish without necessarily causing mortality had received little consideration. Whether or not these studies contributed to earlier implementation of stronger pollution abatement measures on the estuary (in 1972) is perhaps unimportant. What matters is that the abatement measures, combined with restrictions on commercial fishing, have been followed by improved salmon runs into fresh water, and by improved spawning escapement.

Enhancement of commercial catches through delay of migrating fish has not, as far as I am aware, received study before. There are probably other places where it has contributed or is contributing to dangerously heavy fishing of salmon stocks. (It is not inconceivable that there may also be places and species where pollution and consequent delay may contribute to something closer to optimal exploitation of underexploited species.) Whether estuarial pollution in the Miramichi caused any mortality of migrating smolts or adult salmon is not known. When concentrations of toxic chemicals (e.g. pentachlorophenol) and/or biological oxygen demand were, intermittently, high, such mortality could have occurred: identifying it among free-swimming fish in the murky, deep estuarial waters would have been difficult. But bioassay results from caged fish held below the kraft mill (J. A. Dalziel, Environmental Protection Service, Department of the Environment, Halifax, N.S., personal communication) indicate such mortality could have occurred.

Hazard to stocks inherent in the trend towards increased angling pressure also warrants consideration. There has been a widespread opinion that salmon angling, being a somewhat inefficient method of catching the fish, could not possibly pose a threat to stocks. This was probably true 10 or 15 yr ago when stocks were much more abundant and angling pressure probably less intense and persistent. But data offered above indicate that, like commercial fishing, it can be a threat to sufficient recruitment in the face of stocks already depleted by other factors. In New Brunswick this has already received recognition through reduction of daily creel limits and angling seasons since 1970. Complete closure against such recreational fishing may be biologically attractive when early restoration of stocks is an urgent need. But in Canada few salmon fisheries

TABLE 5. Angling pressure and catch of Atlantic salmon, including grilse, on tributaries of the Miramichi system. Approximate mileage of fishing waters from map "Atlantic Salmon Rivers of Canada"[a]; rod days and total catches from Canadian Fisheries Service records. (1 mile = 1.609 km; rod days/km = rod days/mile × 0.62)

	Miles	Rod days	Rod days/ mile	Total catch	Catch/ rod day	Catch/ mile
			1971			
Main Southwest Miramichi	170	16,338	96	6,520	0.40	38.4
Little Southwest Miramichi	65	2,110	32	1,366	0.65	21.0
Dungarvon	45	472	11	126	0.27	2.8
Renous	40	457	11	84	0.18	2.1
Sevogle	35	1,280	37	777	0.61	22.2
Cains	40	–	–	–	–	–
Northwest Miramichi, above fence	*50*	*904*	*18*	*282*	*0.31*	*5.6*
Northwest Miramichi, below fence	7	1,010	144	556	0.55	79.4
			1972			
Main Southwest Miramichi	170	28,422	167	11,778	0.40	69.3
Little Southwest Miramichi	65	4,350	67	3,763	0.87	57.9
Dungarvon	45	834	19	597	0.72	13.3
Renous	40	704	18	471	0.67	11.8
Sevogle	35	1,298	37	1,070	0.82	30.6
Cains	40	1,847	46	1,560	0.84	39.0
Northwest Miramichi, above fence	*50*	*1,230*	*25*	*871*	*0.71*	*17.4*
Northwest Miramichi, below fence	7	1,180	169	782	0.66	111.7
			1973			
Main Southwest Miramichi	170	31,905	188	8,867	0.28	52.2
Little Southwest Miramichi	65	3,898	60	1,377	0.35	21.2
Dungarvon	45	1,549	34	592	0.38	13.2
Renous	40	1,451	36	418	0.29	10.4
Sevogle	35	1,264	36	395	0.31	11.3
Cains	40	1,568	39	253	0.16	6.3
Northwest Miramichi, above fence	*50*	*2,629*	*53*	*1,219*	*0.46*	*24.4*
Northwest Miramichi, below fence	7	2,517	360	793	0.32	113.3

[a] The Atlantic Salmon Association, Montreal, Can.

are privately owned and controlled. Because of difficulties in policing hundreds of miles of forested rivers, such closure could well be followed by uncontrollable poaching. Angler presence on a river tends to retard poaching, so has some value for conserving depleted stocks providing the tribute in salmon taken by the anglers is limited.

Are these studies of Northwest Miramichi salmon pertinent to salmon of the entire Miramichi system? The general Miramichi stock has been subjected to the same pressures in terms of commercial fishing (both distant and at home) and has shown similar, if possibly less severe, declines in abundance (Ruggles and Turner 1973; Turner 1972). Even in the lower part of the Southwest arm of the estuary there appeared to be some, but much less, delay of migratory behavior to make salmon more vulnerable to nets (Elson et al. 1972a). To the extent that Northwest salmon were diverted into the Southwest at the fork of the estuary, Southwest populations must have been augmented. Similarly, Sevogle and Little Southwest stocks must have been diverted at the same place to augment Main Southwest stocks. Sevogle populations were augmented by some salmon of Northwest origin. Such diversions will give rise to impression that the augmented populations are much healthier than in fact they are.

For the system as a whole, measurement of exploitation by angling is by creel census and by recapture of fish tagged in the estuary: significant counts of up-migrating fish are made only on the Northwest. As indicated earlier, acceptance of the assumptions necessary to estimate angling exploitation by recapture of tagged fish is sometimes hazardous. On the Northwest above the counting fence, angler exploitation was frequently estimated as heavier using creel-and-counting-fence data than by using tag–recapture data (Fig. 10, *Upper*). When results of the first method of estimating recreational exploitation have been presented to anglers, their response has almost invariably been that everybody knows the Northwest is subject to much heavier angling pressure than the rest of the system. They are happier with the usually lower estimates available from the tag–recapture system. Recent data from Canadian Fisheries Service records on angling effort and catch data for the important streams of the Miramichi system appear in Table 5. Effort, catch/effort, and catch/mile on the Northwest above the counting fence are well within the ranges indicated for other parts of the system. Densities of young found by electrofishing in other parts of the system are not greatly divergent from those found in the Northwest (G. E. Turner, Resource Development Branch, Department of the Environment, Halifax, N.S., personal communication). The above considerations suggest that complacence with regard to the future of general Miramichi salmon stocks based on limited angler exploitation of these stocks as shown by the tag–recapture system could be illusory. Fence counts and creel censuses, even on one sample tributary, can contribute substantially to increased confidence in estimates of residual spawning stocks.

What of the future for Northwest salmon? A start at recovery does seem indicated by the upward swing in numbers entering the river in 1972 and 1973. Complete recovery for grilse could occur by 1976 if the 2-yr smolt age remains dominant, or 1977 if smolt age reverts to 3 yr with greater interspecific competition on the rearing grounds. To restore the former balance of early- and late-run grilse may take longer because of the more serious recent depletion of late-run grilse parents. Recovery for early-run salmon stocks should be substantial by 1977 or 1978, though not before. But late-run salmon are unlikely to approach pre-1960 levels until the first protected generation (five or six year-classes) has a chance to spawn in normal numbers. This seems unlikely to happen before 1982–84. Until such time, Northwest large salmon could not support any sizeable home commercial fishery without grave risk of repeating a period of depletion like the late 1960s and early 1970s. Whether salmon populations of the rest of the system are in notably better shape than, or only slightly better than, those of the Northwest will emerge in a few years.

Acknowledgments

Covering as it has a period of 24 yr, this study has involved input and cooperation from many people. It is a pleasure to acknowledge their contributions whether mentioned by name or not. C. J. Kerswill, M. W. Smith, and K. R. Allen were, in turn, in charge of salmon investigations of the Atlantic Biological Station, St. Andrews, N.B. until 1967. R. L. Saunders and P. E. K. Symons assumed responsibility for several of the research programs centering around the counting fence, including early phases of experiments involving release of tagged smolts from selectively bred parents. Much of the data could not have been gathered without the dedicated effort of the field staff, under direction of E. J. Schofield since 1957. J. B. Sprague, V. Zitko, and W. V. Carson did the chemical analyses as well as providing encouragement and stimulating discussion. Cooperation of the staffs of the Conservation and Protection Branch and of the Resource Development Branch of the Canadian Fisheries Service was essential and freely given. Candid and helpful comments on their experiences in commercial salmon fishing by H. Williston and A. Scott of the Miramichi Commercial Fishermen's Association are acknowledged with pleasure. W. H. Ketchen and management officers of the Miramichi Timber

Resources kraft mill at Newcastle readily provided information on operational history of the mill. Miss M. Holmes organized and processed much tag return and other data accumulated to 1971, and Miss A. Williamson has continued these operations and assisted in bringing order and analyses to the entire data bank since. P. W. G. McMullon and F. B. Cunningham prepared the diagrams illustrating this study. I, alone, am responsible for any errors, omissions, or misinterpretation of data.

ANDERSON, J. M. 1971. II. Sublethal effects and changes in ecosystems. Assessment of the effects of pollutants on physiology and behaviour. Proc. R. Soc. Lond. Ser. B 177: 307–320.

ANDERSON, J. M., AND P. F. ELSON. 1971. Effect on adult returns of exposure of native wild smolt to sublethal DDT. ICES C.M. 1971/M7: 1–3.

BAUM, E. T., AND A. L. MEISTER, 1971. Fecundity of Atlantic salmon (*Salmo salar*) from two Maine rivers. J. Fish. Res. Board Can. 28: 764–767.

BOCHKOV, A. P. 1970. Forest influence on river flows. UNESCO Bull. Int. Hydrol. Decade. Vol. VI. No. 1: 10–11.

CARSON, W. G., AND W. V. CARSON. 1972. Toxicity of copper and zinc to juvenile Atlantic salmon in the presence of humic acid and lignosulfonates. Fish. Res. Board Can. MS Rep. Ser. 1181: 10 p.

CHUNG, P. 1973. A production function, Canada's Atlantic salmon fisheries. Environ. Can. Res. Stud. No. 2: 1–68.

COOK, R. H., AND R. A. HOOS. 1971. Toxicity monitoring of a primary treated kraft pulp mill effluent at Newcastle, New Brunswick. Dep. Fish. Forest. Can. Fish. Serv. MS Rep. No. 71-1: 1–19.

CÔTÉ, R. P. 1973. A toxicological assessment of a secondary treated kraft mill effluent using static, semi-static and flow-through techniques. Environ. Can. Atl. Reg. Water Pollut. Control Direct. Surveillance Rep. EPS 5-WP-73-3: 1–11.

DIMOND, J. B., A. S. GETCHELL, AND J. A. BLEASE. 1971. Accumulation and persistence of DDT in a lotic ecosystem. J. Fish. Res. Board Can. 28: 1872–1882.

ELSON, P. F. 1957a. Number of salmon needed to maintain stocks. Canadian Fish Culturist 21: 19–23.

1957b. The importance of size in the change from parr to smolt in Atlantic salmon. Canadian Fish Culturist 21: 1–6.

1962a. The Pollett apron seine. J. Fish. Res. Board Can. 19: 93–100.

1962b. Predator–prey relationships between fish-eating birds and Atlantic salmon. Bull. Fish. Res. Board Can. 133: 87 p.

1962c. Atlantic salmon can be maintained in Maritime rivers. Atl. Salmon J. No. 2: 16–18.

1967. Effects on wild young salmon of spraying DDT over New Brunswick forests. J. Fish. Res. Board Can. 24: 731–767.

1973a. Genetic polymorphism in Northwest Miramichi salmon, in relation to season of river ascent and age at maturation and its implications for management of the stocks. Int. Comm. Northwest Atl. Fish. Res. Doc. 73/76. 1–6.

1973b. Limited recovery of depleted Northwest Miramichi salmon follows ban on commercial fishery. Int. Comm. Northwest Atl. Fish. Res. Doc. 73/75: 1–15.

ELSON, P. F., AND C. J. KERSWILL. 1964. Forest spraying and salmon angling. Atl. Salmon J. No. 3: 20–29.

1966. Impact on salmon of spraying insecticide over forests. Adv. Water Pollut. Res. Vol. 1: 55–74.

ELSON, P. F., L. M. LAUZIER, AND V. ZITKO. 1972a. A preliminary study of salmon movements in a polluted estuary. FAO Technical Conference on Marine Pollution and its Effects on Living Resources and Fishing, Rome, Italy, p. 325–330. *In* M. Ruivo [ed.] Marine pollution and sea life. Fishing News (Books) Ltd., London.

ELSON, P. F., A. L. MEISTER, J. W. SAUNDERS, R. L. SAUNDERS, J. B. SPRAGUE, AND V. ZITKO. 1973. Impact of chemical pollution on Atlantic salmon in North America. Int. Atl. Salmon Symp. 1972. Int. Atl. Salmon Found. Spec. Publ. 4: 83–110.

ELSON, P. F., J. W. SAUNDERS, AND V. ZITKO. 1972b. Impact of forest-based industries on freshwater-dependent fish resources in New Brunswick. Fish. Res. Board Can. Tech. Rep. 325: 26 p.

FLIEGER, B. W. 1964. A new method for guiding spray aircraft. Can. Dep. Forest., Forest Entomol. Pathol. Prog. Rep. 20: 1–2.

FORSYTHE, M. G. 1967. Analysis of the 1965 smolt run in the Northwest Miramichi River, New Brunswick. Fish. Res. Board Can. Tech. Rep. 4: 73 p.

1968. Analysis of the 1966 smolt run in the Northwest Miramichi River, New Brunswick. Fish. Res. Board Can. Tech. Rep. 91: 33 p.

GRANT, C. D. 1967. Effects on aquatic insects of forest spraying with phosphamidon in New Brunswick. J. Fish. Res. Board Can. 24: 823–832.

HEWSON, L. C. 1951. A comparison of nylon and cotton gill nets used in the Lake Winnipeg winter fishery. Canadian Fish Culturist 11: 7–9.

HOAR, W. S. 1939. The thyroid gland of the Atlantic salmon. J. Morphol. 65: 257–295.

HOOPER, W. C., AND D. G. HUSTINS. 1973. Recreational salmon angling in New Brunswick. Atl. Salmon J. No. 1: 22–29.

INTERNATIONAL COMMISSION FOR NORTHWEST ATLANTIC FISHERIES. 1972. Proposal regarding conservation of Atlantic salmon. Int. Comm. Northwest Atl. Fish. Doc. 72/33: 2.

1973. Report of the ICES/ICNAF Joint Working Party on North Atlantic Salmon, Copenhagen, 19–23 March, 1973. Int. Comm. Northwest Atl. Fish. Summ. Doc. 73/7: 33.

JONES, J. W. 1959. The salmon. Collins, London. 192 p.

KANID'EV, A. N. 1968. Re-establishment of the Pacific salmon spawning grounds in formerly floatable (refers to log driving — P.F.E.) rivers of the Sakhalin. Izv. TINRO 65: 133–144. (Transl.

from Russian by Fish. Res. Board Can. Transl. Ser. No. 1444: 33 p.) (plus Russian text)

KERSWILL, C. J. 1967. Studies on effects of forest sprayings with insecticides, 1952–63, on fish and aquatic invertebrates in New Brunswick streams: introduction and summary. J. Fish. Res. Board Can. 24: 701–708.

1971. Relative rates of utilization by commercial and sport fisheries of Atlantic salmon (*Salmo salar*) from the Miramichi River, New Brunswick. J. Fish. Res. Board Can. 28: 351–363.

MØLLER, D. 1970. Transferring polymorphism in Atlantic salmon (*Salmo salar*). J. Fish. Res. Board Can. 27: 1617–1625.

MONTREAL ENGINEERING CO. LTD. 1972. Northeastern New Brunswick Mine Water Quality Program. Summary of findings with recommended requirements and procedures. Vol. 1: 92 p.

NETBOY, A. 1968. The Atlantic salmon, a vanishing species. Faber and Faber, London. 457 p.

PALOHEIMO, J. E., AND P. F. ELSON. 1973. The Greenland fishery for Atlantic salmon and Canadian catches. Int. Comm. Northwest Atl. Fish. Res. Doc. 73/85: 000 p.

PAYNE, R. H., A. R. CHILD, AND A. FORREST. 1971. Geographical variation in the Atlantic salmon. Nature 231: 250–252.

PIPPY, J. H. C., AND G. M. HARE. 1969. Relationship of river pollution to bacterial infection in salmon (*Salmo salar*) and suckers (*Catostomus commersoni*). Trans. Am. Fish. Soc. 98: 685–690.

RUGGLES, C. P., AND G. E. TURNER. 1973. Recent changes in stock composition of Atlantic salmon (*Salmo salar*) in the Miramichi River, New Brunswick. J. Fish. Res. Board Can. 30: 779–786.

SAUNDERS, R. L. 1967. Seasonal pattern of return of Atlantic salmon in the Northwest Miramichi River, New Brunswick. J. Fish. Res. Board Can. 24: 21–32.

SAUNDERS, R. L., AND J. B. SPRAGUE. 1967. Effects of copper–zinc mining pollution on a spawning migration of Atlantic salmon. Water Res. 1: 419–432.

SPRAGUE, J. B., AND D. E. DRURY. 1969. Avoidance reactions of salmonid fish to representative pollutants, p. 169–179. *In* Proc. 4th Int. Conf. Advances in Water Pollution Research, Prague.

SPRAGUE, J. B., P. F. ELSON, AND J. R. DUFFY. 1971. Decrease in DDT residues in young salmon after forest spraying in New Brunswick. Environ. Pollut. 1: 191–203.

SPRAGUE, J. B., P. F. ELSON, AND R. L. SAUNDERS. 1965. Sublethal copper–zinc pollution in a salmon river — a field and laboratory study. Int. J. Air Water Pollut. 9: 531–543.

SPRAGUE, J. B., AND B. A. RAMSAY. 1965. Lethal levels of mixed copper–zinc solutions for juvenile salmon. J. Fish. Res. Board Can. 22: 425–432.

TURNER, G. E. 1972. Exploitation of Miramichi Atlantic salmon based on smolts tagged in 1968, 1969 and 1970. Int. Comm. Northwest Atl. Fish. Fish Redbook. Part III: 59–64.

WILDISH, D. J., W. G. CARSON, AND W. V. CARSON. 1971. The effect of humic substances on copper and zinc toxicity to salmon, *S. salar* L. Fish. Res. Board Can. MS Rep. Ser. 1160: 8 p. (plus Appendices)

Benthos and Allochthonous Organic Matter in Streams[1]

H. B. N. Hynes, N. K. Kaushik,[2] M. A. Lock, D. L. Lush,[3] Z. S. J. Stocker,[4]
R. R. Wallace,[5] and D. D. Williams

Department of Biology
University of Waterloo, Waterloo, Ont.

Hynes, H. B. N., N. K. Kaushik, M. A. Lock, D. L. Lush, Z. S. J. Stocker, R. R. Wallace, and D. D. Williams. 1974. Benthos and allochthonous organic matter in streams. J. Fish. Res. Board Can. 31: 545–553.

Investigations into the vertical distribution of stream animals by means of a coring technique have demonstrated that they could be found many decimeters down in the gravel; a maximum of 17% was found in the top 5 cm.

Sampling of arctic streams revealed that chironomid larvae comprised 70–80% of the numbers in the benthos and that their rate of drift did not vary with the time of day.

Life history studies of stream invertebrates have demonstrated clear seasonal patterns in Canada. Work has been done on several mayflies and stone flies, some Chironomidae, and two species of *Gammarus*. Currently the life histories of the stone flies of southern Australia are being investigated in which the seasonality is much less marked.

After the experimental application of the blackfly larvicide Methoxychlor to two rivers, a catastrophic drift of invertebrates occurred and larvicide residues were detected up to 8 wk after application.

Work on the decomposition of autumn-shed leaves in water has included the responses to temperature and to additional nutrients (N and P). The effect of nutrient addition was to increase the amount of nitrogen in the leaf after incubation, but temperature affected only the rate of decomposition. Determination of the relative importance of bacteria and fungi in decomposition, was studied with use of antibiotics, and food preference of *Gammarus* for several leaf species was determined.

A considerable portion (up to 40%) of the autumn-shed leaf is water-soluble, and the way in which it is made available to stream animals was investigated. One process, its conversion into particles, appears to involve mechanisms similar to those found in soils, i.e. by formation of organic/metal complexes. Using infrared spectroscopy, attempts have been made to characterize the laboratory and field-produced particles. Field investigations have also demonstrated large-scale fluctuations, during only a few hours, of dissolved and particulate organic matter in the water.

These findings are considered in relation to general stream ecology.

Hynes, H. B. N., N. K. Kaushik, M. A. Lock, D. L. Lush, Z. S. J. Stocker, R. R. Wallace, and D. D. Williams. 1974. Benthos and allochthonous organic matter in streams. J. Fish. Res. Board Can. 31: 545–553.

Des recherches sur la distribution verticale d'animaux de cours d'eau à l'aide d'une technique de carottage démontrent que ces organismes se trouvent à des profondeurs de plusieurs décimètres dans le gravier; on en a recueilli 17% dans les 5 cm supérieurs.

L'échantillonnage de cours d'eau arctiques démontre que les larves de chironomides constituent 70–80%, en nombre, du benthos, et que leur vitesse de dérive ne varie pas suivant l'heure du jour.

L'étude du cycle biologique d'invertébrés fluviatiles démontre qu'il existe de clairs schémas saisonniers au Canada. Nous avons étudié plusieurs espèces de phryganes et de

---

[1] This paper, part of a special issue that comprises a comprehensive review of Limnology in Canada, was prepared to mark the 19th Congress of the International Association of Limnology (SIL), in Winnipeg, Man., during August 1974.

[2] Present address: (N. K. K.) Department of Environmental Biology, University of Guelph, Guelph, Ont.

[3] Present address: (D. L. L.) Beak Consultants Ltd., Suite 3, 306 Rexdale Blvd., Toronto, Ont.

[4] Present address: (Z. S. J. S.) Delaselle College Oaklands, 131 Farnham, Toronto, Ont.

[5] Present address: (R. R. W.) Department of the Environment, Environmental Protection Service, P.O. Box 2310, Yellowknife, N.W.T.

Printed in Canada (J3264)

perles, quelques Chironomidae et deux espèces de *Gammarus*. On est présentement à étudier le cycle biologique des perles de l'Australie méridionale, chez lesquelles les variations saisonnières sont beaucoup moins prononcées.

Après application expérimentale de Méthoxychlore, larvicide pour simulies, on a constaté un dérive catastrophique d'invertébrés et détecté des résidus du larvicide jusqu'à 8 semaines après application.

Des travaux sur la décomposition des feuilles tombant dans l'eau en automne ont porté entre autres sur les réponses à la température et à l'addition de substances nutritives (N et P). L'addition de substances nutritives a eu pour effet d'augmenter la quantité d'azote dans la feuille après incubation, mais la température n'a fait qu'affecter la vitesse de décomposition. A l'aide d'antibiotiques, nous avons déterminé l'importance des bactéries et des champignons dans la décomposition. Nous avons également déterminé les préférences alimentaires de *Gammarus* en rapport avec plusieurs espèces de feuilles.

Une portion considérable (jusqu'à 40%) des feuilles tombant en automne est soluble dans l'eau, et nous avons étudié la façon dont cette portion peut être utilisée par les organismes fluviatiles. Un processus, sa conversion en particules, semble impliquer des mécanismes semblables à ceux observés dans les sols, i.e. formation de complexes matière organique/métaux. A l'aide d'un spectroscope infrarouge, nous avons tenté de définir les caractéristiques des particules produites au laboratoire et sur le terrain. Les travaux sur le terrain ont également démontré de grandes variations, pendant quelques heures seulement, de la matière organique dissoute et particulaire.

Nous examinons ces découvertes dans le contexte général de l'écologie des cours d'eau.

Accepted December 31, 1973

WORK in our laboratory at Waterloo has centered around the benthos of streams and the source of the energy that supports it in a habitat that is often short of primary producers. During our work we have investigated the vertical distribution of the benthos within the substratum, the life histories and growth patterns of a considerable number of invertebrates, conditions in some high arctic streams, the fate of the autumn-shed leaves that fall into streams and their attractiveness to invertebrates as food, and the conversion of the leachate from such leaves into particles by chemical or biological action. One of us has also investigated the effect of the blackfly larvicide Methoxychlor on the stream biota.

Several publications have resulted from this work (e.g. Kaushik and Hynes 1968, 1971; Bishop and Hynes 1969; Hynes and Kaushik 1969; Coleman and Hynes 1970a, b; Harper and Hynes 1970, 1972; Spence and Hynes 1971; Hynes and Harper 1972; Harper 1973) and others are in press or in preparation. This paper deals mostly with our more recent results and with some of our ongoing studies.

Studies on the Hyporheic Fauna of Stream Beds

It has been assumed until fairly recently that all the benthic invertebrates of streams occur within a few centimeters of the substrate surface. However, some recent studies have shown that significant populations of these animals occur deeper in the substrate, consequently, conventional benthic samplers may fail to measure the total biomass because of shallow sampling methods (usually around 5 cm). Our most recent sampler, one of a long evolutionary series, was a standpipe case that allowed 25-ml cores of gravel to be taken from depths of up to 100 cm in streams with deep gravel beds. Results showed the subbenthic (hyporheic) fauna of the Speed River, Wellington County, Ontario to consist of two distinct groups, a large "occasional" fauna consisting of representatives of most of the surface benthos, particularly chironomid larvae, and a much smaller, perhaps endemic, fauna limited to some mites and copepod crustacea. Total numbers of benthic organisms in the Speed River were estimated to range between approximately 180,000 and 800,000/m^3 depending on the time of year. Of these, only a maximum of 17% could be attributed to the top 5 cm of substrate. Figure 1 indicates that a similar situation occurs in at least two other rivers. Temporal sampling of the Speed River suggested that the invertebrates may undertake vertical migrations in response to periodic changes in the interstitial environment.

On the strength of the above findings, work is now proceeding on applying the significance of these interstitial populations to the recolonizing of the surface benthos, should it be destroyed by abnormal stream flow phenomena such as spates or droughts. There is some evidence to suggest that the hyporheic fauna may act as a reserve population in such circumstances.

ARCTIC STREAM STUDY

The arctic streams study was carried out at the site of one of the Canadian I.B.P. Projects on Char Lake. The purpose of the study was to gather information on the composition of the benthos and its drift activity.

Bottom-sampling demonstrated that 70–80% of the benthos by numbers was composed of Chironomid larvae, the next largest group, the Enchytraeidae comprised 10–20%, the remainder were Nematoda, Ostracoda, *Cyclops*, *Atthyella* and others. The chironomids were divided into one member of the Diamesinae, *Diamesa* sp., and four Orthocladinae, *Diplocladius* sp., *Orthocladius* sp., *Lymnophyes* sp. and *Metriocnemus* sp. An interesting observation on the chironomid distributions throughout the sampling stations was that if *Diamesa* were present the Orthocladinae were absent or rare. On the other hand, if *Diamesa* were absent then the various representatives of the Orthocladinae were approximately equally represented (Fig. 2).

Work on the drift of the chironomids demonstrated that the amount of drift showed an exponential relation to current velocity. If the velocity component of the drift is removed (log number of animals/mean velocity) and this number is plotted against time of day, the time of day has little influence on the drift (Fig. 3). This observation was confirmed by a field experiment in which a section of stream was submitted to periods of artificial darkness. In these experiments, the drift rate was

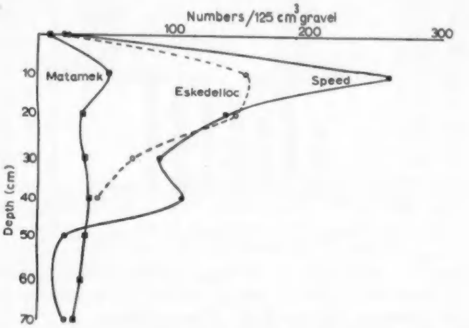


FIG. 1. Plot of the total numbers of animals per 125 cm^3 of gravel vs. depth for three Canadian rivers.

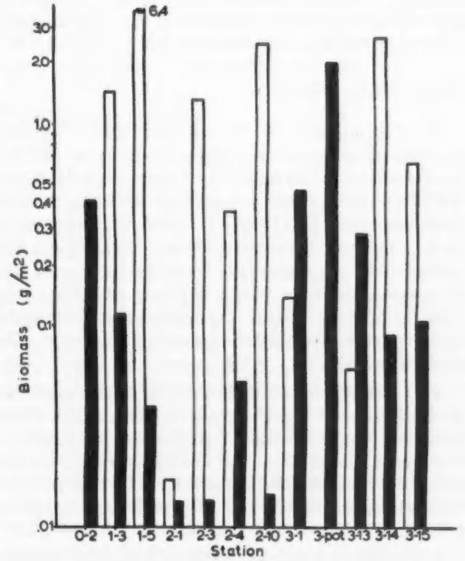


FIG. 2. The distribution of chironomid larvae expressed as biomass (g/m^2) at several stations.

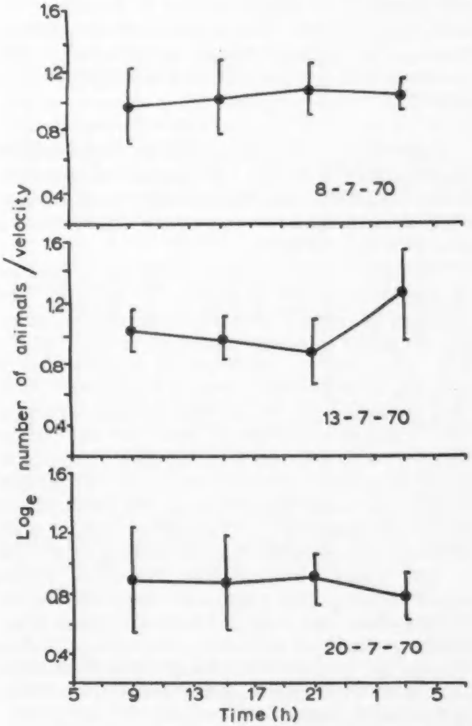


FIG. 3. The product of logarithm of the number of animals caught in driftnets and velocity^{-1} plotted against time of day.

again found to be influenced by changes in the light regime.

Probably an important factor related to the drift activity of the benthos is catastrophic drifting induced by erosion. Throughout the year extreme spates will exert their effect on the benthos, the effect being greatest during the spring snow melt. Cogley (1971) estimated that 99% or more of the annual erosion takes place during this period. The top 5 cm of the benthos is likely to be taken entirely out of the habitat during this period. It would seem that vertical distribution within the substratum is important in the high arctic also.

EFFECTS OF METHOXYCHLOR ON THE STREAM BIOTA

At the time that the studies for this work were begun, the literature on aquatic biology contained many reports of field and laboratory studies on the effects of various insecticides on the larvae of Simuliidae. However, comparatively few studies were available on the effects of such treatments on other aquatic animals in streams so treated.

It was proposed to undertake a program of studies which might provide an overview of the problems and serve as a basis for further detailed studies.

Chalk River — The dispersion of Methoxychlor and Rhodamine B dye was studied using fluorometry and chromatographic analyses. Accumulation of Methoxychlor was studied in laboratory and field experiments.

The Chalk River was treated with an oil solution of Methoxychlor (0.79 µg/liter for 15 min). The numbers of simuliid larvae drifting as a result of the treatment reached maximum values 60 min after beginning the treatment at stations 275 m and 550 m downstream from the treatment point (Fig. 4). Peak values of drifting simuliids decreased with distance downstream. Most of the larvae began to drift after the Methoxychlor had passed downstream. No Methoxychlor could be detected in larvae or moss collected from the Chalk River before the treatment. Drifting larvae caught after the treatment contained residues ranging from 0.24 to 2.57 mg/kg of larvae (Fig. 4). Larvae which began drifting later generally contained more Methoxychlor than those drifting sooner after treatment. Residues of Methoxychlor were detected in moss and grasses in the stream up to 8 wk after treatment. Residues ranged from 7.4 to 34.6 µg/kg (wet weights).

Laboratory experiments indicated that simuliid larvae concentrated particulate formulations of Methoxychlor more efficiently than ethanol formulations; residue values reached as high as 2310 µg/kg. Trichoptera larvae concentrated Methoxychlor to levels as high as 1563 µg/kg. and ethanol formulations were concentrated to higher levels than particulate formulations by trichopterans.

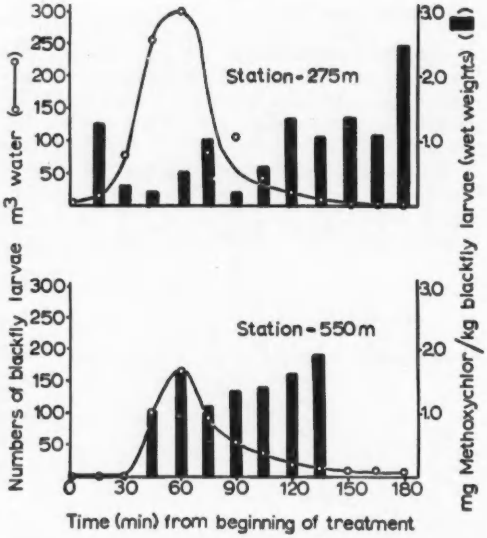


FIG. 4. Numbers of drifting blackfly larvae per m³ of water and the concentration of Methoxychlor in the larvae at various times after treatment.

SPEED RIVER STUDY

In experiments in the Speed River, Ontario, wooden boards were positioned over a uniform gravel riffle so as to form two channels in midstream. Driftnets were placed at the downstream ends of both channels, and in one channel at the upstream end. Thus one channel was open to recolonization drift from upstream and the other was not. The channels were treated with 0.75 mg Methoxychlor/liter for 15 min. Tray, kick, and emergence samples were collected from both channels before and after the treatments.

The insecticide caused a catastrophic drift of invertebrates off the channels that lasted for about 90 min (Fig. 5). Severe losses of invertebrates in the upper layers of gravel (particularly the larger, heavier specimens) were partially offset by animals that remained unharmed in the lower layers of gravel.

Invertebrates recolonized the channels by moving in from upstream areas and possibly by moving into the upper layers of gravel from the lower levels.

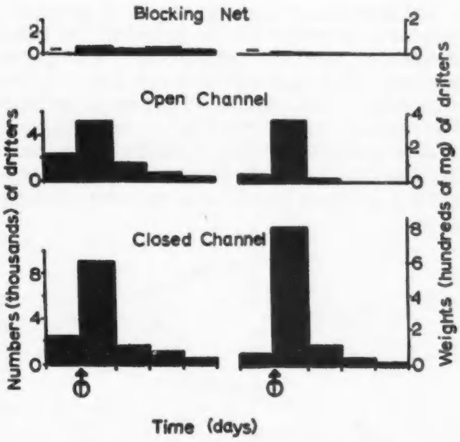


FIG. 5. Total amounts of drifting insects caught before and after the treatment with Methoxychlor. Ordinate: the mean numbers and weight of insects caught. Abscissa: approximate 24-h periods. Ⓣ, the time of treatment.

It is evident from the Chalk River study that the concentration of Methoxychlor normally used (0.75 mg/liter) would seem to be in some cases in excess of that required to significantly affect the blackfly larvae. It is equally obvious from the Speed River study that the insecticide is far from selective in its action and has a catastrophic effect on a major part of the stream animals.

LIFE HISTORY STUDIES

Our studies of life histories have shown that, as was already known for Europe and to a much lesser extent for North America, most stream insects show clear seasonal patterns. These have been discussed elsewhere (Hynes 1970). We have, however, established that at least one local *Gammarus* takes 2 yr to mature, that the well-known winter stone flies of North America undergo a nymphal diapause, a phenomenon that was previously known only of one European species, and that some Chironomidae migrate vertically in the gravel during their larval lives.

Currently one of us is studying the life histories of stone flies in southern Australia, where the uncertain climate and the evergreen forest, with its entirely different input of allochthonous material into streams, provide a valuable contrast to conditions here. It seems that patterns of eclosion, and of growth and emergence, are noticeably different to those of the northern temperate zone.

AUTUMN-SHED LEAVES IN RELATION TO STREAM ECOLOGY

Our earliest study of the input of allochthonous organic matter into streams, concerned the fate of autumn-shed leaves. The original investigations were based on the hypotheses that newly shed leaves would be low in protein content and that they became available to the benthos only through microbial growth. This work formed the basis of two papers (Kaushik and Hynes 1968, 1971), and these will be summarized.

Autumn-shed leaves of elm, alder, oak, beech, and maple were separately incubated at 10 C and at 20–22 C for different time intervals in stream water enriched either with a nitrogen source only, or with both nitrogen and phosphorus sources, or in water without added nutrients as a control. As expected, the effect of temperature was to alter the rate of decomposition as indicated by protein and nitrogen levels. At both temperatures, the controls showed only small changes in protein and nitrogen values, but the leaves supplied with nutrients showed statistically significant increase values, which were larger when both nutrients were added (Fig. 6 and 7). To determine whether there was an increase in the absolute quantity of nitrogen, the amount of nitrogen found in the leaves at the end of each sampling time was calculated as a percentage of the initial weight. At both temperatures the controls gained no nitrogen, but the leaves kept in enriched waters showed significant increases in the absolute quantity of nitrogen, and this was more pronounced when both the nutrients were added (Fig. 7). However, this uptake or immobilization of exogenous nitrogen was confined to a certain level which was attained in 1 to 2 wk, depending on temperature. Once this level was reached, only small further changes occurred. Also, whereas the availability of phosphorus altered the quantity of immobilized nitrogen, the temperature affected only the rate of immobilization. Elm and maple leaves decomposed much faster and showed larger increases in protein and nitrogen contents, as compared with the remaining types. Results from field experiments carried out in two streams showed the same general pattern of events.

To determine the relative importance of bacteria and fungi, four sets of elm leaf discs were incubated in enriched stream water. To the first set, the control, no antibiotics were added, the second received both antifungal and antibacterial antibiotics, the third had only antifungal antibiotics, and the fourth only antibacterial antibiotics. Fungi appeared to be the main agents for leaf degradation and for raising the protein and nitrogen content (Fig. 8).

Given a choice between several leaf species. animals feed preferentially on some species, and the order of choice is the same as the order of the rate of decay — elm, maple, alder or oak, beech. Our experiments also showed quite conclusively that animals fed preferentially on leaves on which microorganisms were growing. There is little doubt therefore, that saprophytic fungi are the major attractants and the major source of protein.

The importance of leaf litter as food for aquatic organisms probably lies in providing an energy source for microbial growth and, through the preference of animals for leaves that support microorganisms, a vast resource of energy is profitably exploited in streams, leading to secondary and tertiary production. Also it appears that leaves can alter the quality of stream water, not only by exerting oxygen demand and releasing dissolved

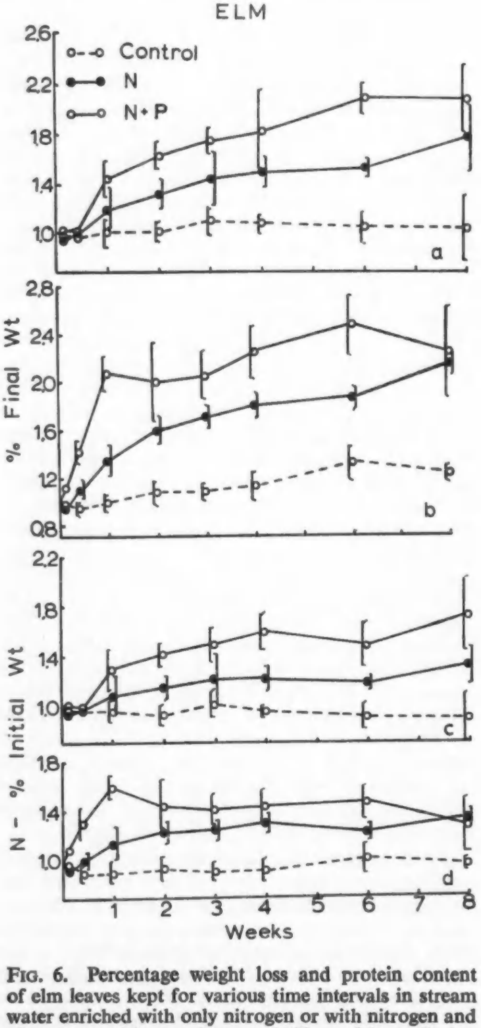


FIG. 6. Percentage weight loss and protein content of elm leaves kept for various time intervals in stream water enriched with only nitrogen or with nitrogen and phosphorus. Mean values ± 95% confidence limits; (a) and (c) at 10 C and (b) and (d) at 20–22 C.

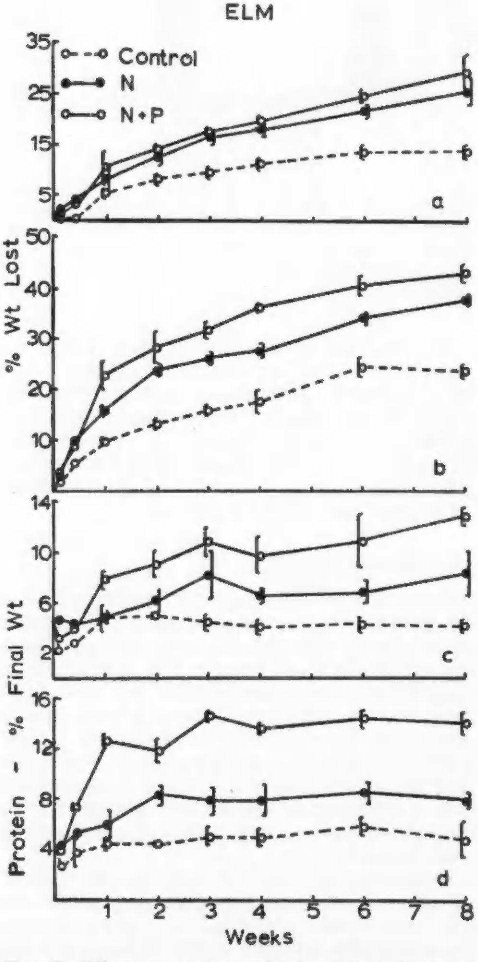


FIG. 7. Nitrogen content of elm leaves kept for various time intervals in stream water enriched with only nitrogen or with nitrogen and phosphorus. Mean values ± 95% confidence limits; (a) and (c) at 10 C and (b) and (d) at 20–22 C.

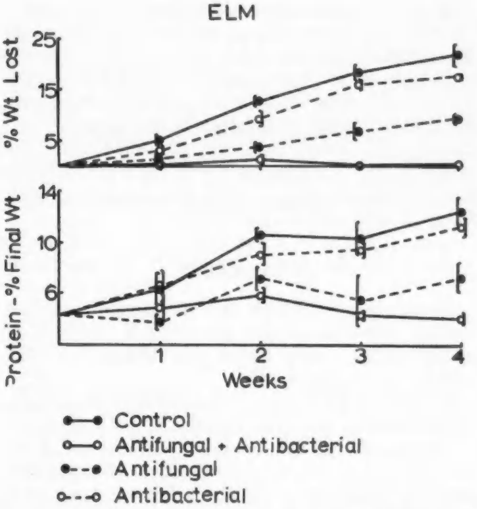


FIG. 8. Percentage weight loss and protein content of elm leaves kept at 10 C for various time intervals in enriched stream water and treated with different antibiotics. Mean values ± 95% confidence limits.

substances, but also by acting as a "sink" for nutrients.

Our work with leaves and our demonstration of the important role of fungi in their decomposition and their palatability to invertebrates, has led to an interest in this subject by some mycologists in our department. In a study that we expect will soon be published, they have shown that fungi are indeed important in attracting animals to feed on decaying leaves and that different species vary in attractiveness. This variation is sufficiently great to control the palatability to *Gammarus* of various species of leaf, and different groups of fungi appear to be active at different seasons. This demonstration of selective feeding within "detritus" may be of importance in distributional studies of *Gammarus*, and similar feeding activity may be found in other detritivores.

SUSPENDED AND DISSOLVED ORGANIC MATTER STUDIES

Early in the study of leaf decomposition, it was evident that a considerable proportion of the autumn-shed leaf was water-soluble and that it leached out in a matter of a few days. Other investigators have also noted this phenomenon; it can involve up to 40% of the original weight. This represents a potentially large source of energy for the stream biota.

A major aspect of this problem was the form in which this soluble material was made available to the benthos. One possible process was the conversion of the soluble material into particles, as is known to occur in sea water. This appeared to involve both abiotic and biotic factors. Physical agitation (turbulence) produces particles from the dissolved organic matter in the laboratory, but some field evidence suggests that this may not be

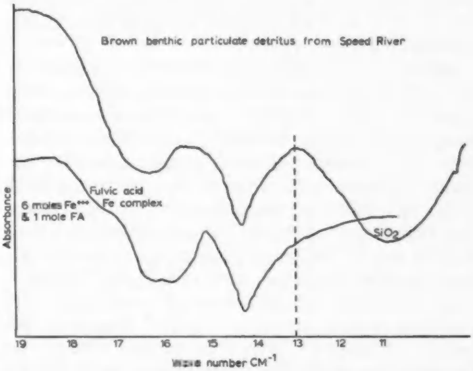


FIG. 9. Infrared spectra of a laboratory-produced fulvic acid and iron complex (from Schnitzer 1969) and brown benthic particulate detritus from the Speed River.

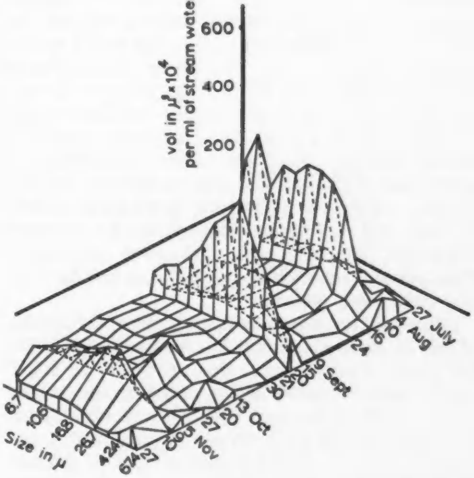


FIG. 10. Three dimensional plots of particle size, their relative volumes and time of year in a small hardwater stream.

an important process in streams. However, the formation of particles by the complexing of dissolved organic matter with divalent metals, as in the humus/metal complexes described by Schnitzer (1969), are probably also found in streams. By using initially sterilized leaf/water, it was possible to obtain within 1 h, precipitates that on visual inspection appeared to be similar to the brown amorphous detritus found in the field. Analyses were made of the particle size-frequency distribution with time, of several species of leaves under varying conditions of pH. The findings of these investigations are in Lush and Hynes (1974).

Attempts have also been made to characterize the organic detritus in the laboratory and in the field. The use of infrared spectroscopy produced comparable spectra between detritus from a local river and the metal/organic complexes of known weight of fulvic acid produced by Schnitzer (1969) (Fig. 9). Infrared spectrographs of laboratory material showed a much greater variability. This may be due to their recent origin as compared with field material which will have undergone "ageing."

Investigations of the levels of particulate and dissolved organic matter in the field have involved weekly analyses of several hardwater streams in the Waterloo area. The particulate organic matter has been shown to vary greatly over short periods of time (Fig. 10). An analysis of the particulate organic fraction showed the protein content to vary between 0.5 and 10%. The lower values were found to occur just after rainstorms and were probably due to dilution. However, the highest absolute values of suspended protein occurred at this time. The high values of 10% are found within a week after the rain. The levels of particulate organic matter varied from a high of about 60 mg/liter to a low of less than 1 mg/liter and the streams showed fluctuations of this magnitude overnight during summer rainstorms. Other measurements were made of total soluble organic material, soluble protein, soluble carbohydrate, particulate carbohydrate, and particulate chlorophylls. All of these substances showed large short-term variations. This type of fluctuation should be taken into account when sampling streams.

Other field investigations have involved the uptake of leaf leachate in a small hardwater stream (TDS 200 ppm). To investigate this, leachates of sugar maple were prepared by autoclaving the maple leaves in distilled water. The leachate was added to the stream during a 20-min period, raising the concentration of dissolved organic matter (DOM) at the point of addition from 4 to 40 ppm. Water samples were collected at a weir downstream and the progress of the DOM as it passed down the stream was followed by use of an internal low-level sodium ion tracer. The results of these experiments showed that up to 75% of the added leachate had disappeared from the water column within 1 h and a distance of 30 m. The same experiment was conducted with other species such as cedar, and with these also a large percentage of the leachate had disappeared. This rapid loss of DOM from the water clearly demonstrates that it has a considerable role in stream ecology. This phenomenon is now being investigated in the laboratory.

Conclusions

Although it is difficult to summarize our diverse studies, they are all directed towards the goal of understanding more about the clearly complex ecology of stream systems.

We feel we have shown that the hyporheic zone, which extends for tens of centimeters below the gravel–water interface, is of great importance, both as a refuge and source of recolonizers after disaster, and as a locale for parts of the life histories of a variety of species. It also presents a still unsolved challenge to quantitative sampling, although we believe that our newest sampler (Williams and Hynes 1974) is at least offering some hope. However, research is continuing in this area.

We also think that we are beginning, dimly, to understand something about the trophic relations of streams to their watersheds. The role of autumn-shed leaves has received considerable attention. However, much more work is required on suspended and dissolved organic matter, particularly with respect to its origin. Autumn-shed leaves and primary producers are two sources, but it is becoming evident that the groundwater zone may be an important agent, in particular the soil zone. Likely under flood conditions large quantities of organic material resulting from terrestrial breakdown will find their way into the stream system. These processes, coupled with data on the role of feces, the micro-flora and fauna, and water chemistry, are leading us to a point where the detritus concept and production can be investigated mechanistically. We are now beginning to look at these things.

Acknowledgments

We gratefully acknowledge financial support from the National Research Council of Canada.

Bishop, J. E., and H. B. N. Hynes. 1969. Downstream drift of the invertebrate fauna in a stream ecosystem. Arch. Hydrobiol. 66: 59–90.

Cogley, J. G. 1971. Hydrological and geomorphological investigations on a high latitude drainage basin: "Jason's Creek," South-West Devon Island, N.W.T. M.Sc. Thesis. McMaster Univ., Hamilton, Ont. 141 p.

Coleman, M. J., and H. B. N. Hynes. 1970a. The vertical distribution of the invertebrate fauna in the bed of a stream. Limnol. Oceanogr. 15: 31–40.

1970b. The life histories of some Plecoptera and Ephemeroptera in a southern Ontario stream. Can. J. Zool. 48: 1333–1339.

Harper, P. P. 1973. Life histories of Nemouridae and Leuctridae in southern Ontario. (Plecoptera). Hydrobiologia 41: 309–356.

Harper, P. P., and H. B. N. Hynes. 1970. Diapause in the nymphs of Canadian winter stoneflies. Ecology 51: 925–927.

1972. Life histories of Capniidae and Taeniopterygidae (Plecoptera) in southern Ontario. Arch. Hydrobiol. Suppl. 40: 274–314.

Hynes, H. B. N. 1970. The ecology of running waters. Liverpool Univ. Press, Liverpool. 555 p.

Hynes, H. B. N., and F. Harper. 1972. The life histories of *Gammarus lacustris* and *G. Pseudolimnaeus* in southern Ontario. Crustaceana Suppl. (Leiden) 3: 329–341.

Hynes, H. B. N., and N. K. Kaushik. 1969. The relationship between dissolved nutrient salts and protein production in submerged autumnal leaves. Verh. Int. Ver. Limnol. 17: 95–103.

Kaushik, N. K., and H. B. N. Hynes. 1968. Experimental study on the role of autumn-shed leaves in aquatic environments. J. Ecol. 56: 229–243.

1971. The fate of the dead leaves that fall into streams. Arch. Hydrobiol. 68: 465–515.

Lush, D., and H. B. N. Hynes. 1974. The formation of particles in freshwater leachates of dead leaves. Limnol. Oceanogr. 18: 968–977.

Schnitzer, M. 1969. Reactions between fulvic acid, a soil humic compound and inorganic soil constituents. Soil Sci. Soc. Am. Proc. 33: 75–81.

Spence, J. A., and H. B. N. Hynes. 1971. Differences in benthos upstream and downstream of an impoundment. J. Fish. Res. Board Can. 28: 35–43.

Williams, D. D., and H. B. N. Hynes. 1974. The occurrence of benthos deep in the substratum of a stream. Freshwater Biol. 4: 1–23.

Limnological Conditions in Five Small Oligotrophic Lakes in Terra Nova National Park, Newfoundland[1]

JOSEPH J. KEREKES

Department of the Environment
Canadian Wildlife Service, c/o Biology Department, Dalhousie University, Halifax, N.S.

KEREKES, J. J. 1974. Limnological conditions in five small oligotrophic lakes in Terra Nova National Park, Newfoundland. J. Fish. Res. Board Can. 31: 555–583.

Five oligotrophic lakes in Terra Nova National Park, Newfoundland, varying in mean depth (1.06–9.22 m), in water renewal rate (0.2–20.7 times per annum), in salinity (18.2–42.6 mg/liter), in total phosphorus (0.1–0.6 mg-at P/m^3), and in chlorophyll *a* concentration (0.5–3.2 mg/m^3), were investigated for 17 mo in 1969 and 1970. Hypolimnetic oxygen deficits ranged between 111 and 217 mg O_2 per m^2/day. Low levels of nutrients, reduced solar radiation, and low underwater light penetration, owing to excessive cloudiness and high water color, seriously limited planktonic primary production. The relation between primary production at optimum light, and water renewal per annum, appeared to be curvilinear when the rate of primary production began to decline above an optimum water renewal rate. The seasonal and annual variations in water color and salinity were dependent on the rate of water renewal, but other lakes on the catchment areas modified that relation. Winter road salting operations within the catchment area caused a considerable increase in salinity, total phosphorus concentration, and primary production in one lake. A new morphometric index which reflects the littoral effect on basin volume was proposed.

KEREKES, J. J. *1974. Limnological conditions in five small oligotrophic lakes in Terra* Nova National Park, Newfoundland. J. Fish. Res. Board Can. 31: 555–583.

Nous avons étudié, sur une période de 17 mois en 1969 et 1970, cinq lacs oligotrophes du parc national Terra Nova, Terre-Neuve, variant sous le rapport de la profondeur (1.06–9.22 m), de la vitesse de renouvellement de l'eau (0.2–20.7 fois par année), de la salinité (18.2–42.6 mg/litre), du phosphore total (0.1–0.6 mg-at P/m^3) et de la teneur en chlorophylle *a* (0.5–3.2 mg/m^3). Les déficits d'oxygène dans l'hypolimnion s'échelonnent de 111 à 217 mg O_2 par m^2/jour. De bas niveaux de substances, une faible radiation solaire et pénétration de la lumière dans l'eau, par suite d'une nébulosité excessive et de la forte coloration de l'eau, limitent sérieusement la production primaire du plancton. La relation entre la production primaire sous éclairage optimal et le renouvellement annuel de l'eau semble être curvilinéaire quand le taux de production primaire commence à diminuer au-dessus d'un taux optimal de renouvellement de l'eau. Les variations saisonnières et annuelles de la couleur de l'eau et de la salinité dépendent du taux de renouvellement de l'eau, mais d'autres lacs dans le bassin hydrographique viennent modifier cette relation. L'épandage de sel sur les routes en hiver dans le bassin hydrographique entraîne une augmentation considérable de la salinité, de la teneur en phosphore totale et de la production primaire dans un des lacs. Nous proposons un nouvel indice morphométrique tenant compte de l'effet du littoral sur le volume du bassin.

Accepted December 31, 1973

ALTHOUGH insular Newfoundland is extremely rich in fresh water, these resources, in the main, have remained virtually unknown (Smith 1963). More recently, however, this has begun to change (see Davis 1972). Newfoundland has some deep, large lakes ($\bar{z}_m > 70$ m), some of which are presently under investigation (Kerekes and Schwinghamer 1973), but the majority of the lakes are small. This paper describes selected physico-chemical characteristics and morphometric factors, and relates them to limnetic phytoplankton production in five small lake basins in eastern Newfoundland. It is the second paper in a series, based on a detailed report (Kerekes 1972). Various aspects of primary

---

[1] This paper, part of a special issue that comprises a comprehensive review of Limnology in Canada, was prepared to mark the 19th Congress of the International Association of Limnology (SIL), in Winnipeg, Man., during August 1974.

Printed in Canada (J3265)

production in these lakes are given elsewhere (Kerekes 1974a, b).

The lakes lie in Terra Nova National Park on the northeastern coast of Newfoundland (Table 1). A detailed study of the general and structural geologic features of the area is given by Jenness (1963). The study basins lie entirely on Precambrian rocks at the eastern extremity of the North American taiga. The Atlantic Ocean, with the cold Labrador current, is the major factor controlling the climate of the area. The summers are cool, the winters moderately cold. Average yearly mean temperature is 4.3 C. The long-term average precipitation is 1.06 m, of which 0.70 m is rain (Anon. 1970). The average water surplus is 0.56 m (Hare 1952).

In general, a standing freshwater body is called a "pond" in Newfoundland. The term "lake" is usually reserved for large bodies of water greater than 100 km^2 in surface area. The terms "lake" and "pond" are often used ambiguously by limnologists in the absence of precise definition (Reid 1961; Reeves 1968; Anderson 1971). In this paper, Reeves' (1968) definition of "lake," "pond," and "bog" is accepted. When the official names of the study lakes are not used they are termed as lakes because they are too deep to permit the growth of rooted emergent vegetation across the water expanse. The term "bog" refers to any water saturated depression which contains an accumulation of *Sphagnum*.

The lake shores are rocky. Only sparse growth of aquatic macrophytes, mainly *Eriocaulon septangulare* With., *Potamogeton oakesianus* Robbins, *P. praelongus* Wulfen, and *Nuphar variegatum* Engelm. was observed in Pine Hill, Yudle North, and Bluehill North ponds, and these macrophytes were rare in Minchin and Bluehill South ponds (Kerekes 1968a).

Brook trout (*Salvelinus fontinalis*) and American eel (*Anguilla rostrata*) occur in all lakes, while landlocked populations of Arctic char (*Salvelinus alpinus*), Atlantic salmon (*Salmo salar*), and smelt (*Osmerus mordax*) were found in the two deepest lakes.

Methods

RESEARCH PERIOD

The sampling program commenced in April 1969, and was concluded at the end of August 1970. The frequency of sampling varied through the program with the availability of field assistance and weather conditions. The sampling program was the most intensive during the summer of 1969, when each lake was sampled at least twice a month between June and September. However, Bluehill North, Bluehill South, Pine Hill, and Yudle Ponds were sampled three or four times in some months during this period. In total, sampling periods were: Bluehill North, 14; Bluehill South, 19; Pine Hill, 33; Minchin, 16; and Yudle North, 25.

PHYSICAL AND CHEMICAL PROCEDURES

All sampling was done from small boats attached to the firmly anchored station marker, at approximately the deepest point of the lake.

Water samples for chemical analysis taken from surface waters were collected directly into polyethylene bottles just below the surface, but subsurface samples were taken with a Van Dorn 2–liter nonmetallic sampler except in Pine Hill Pond, where a 1–liter sampler was used at 4- and 5-m depths. Some of the measurements taken at 5 m, and to a lesser extent at 4 m, in Pine Hill Pond have doubtful accuracy owing to a possible sampling error caused by the Van Dorn samples because of the sharp stratification.

Chemical analysis for inorganic constituents such as Ca^{++}, Mg^{++}, Na^{+}, $SO_4^{=}$, Cl^{-}, was done by the laboratory of Energy, Mines and Resources, Inland Waters Branch, Water Quality Division at Moncton, N.B. All samples were filtered through 0.8 μ pore diameter Millipore filters in the field laboratory prior to shipment for analysis. Analysis was completed usually not later than 10 days after sampling.

Total alkalinity was determined potentiometrically for samples of 250 ml as recommended (Am. Public Health Assoc. 1965) for soft waters low in alkalinity. This procedure compared favorably with total alkalinity determinations done by end point and conductometric titrations during the early phase of this study.

TABLE 1. Location, surface elevation, and horizontal distance from the sea for four lakes in Terra Nova National Park, Nfld. Bluehill and Yudle ponds consist of two basins each.

Pond	Elevation (*m*)	Latitude	Longitude	Distance from sea (*km*)
Bluehill	52	48°36′N	53°56′W	1.3
Minchin	9	48°33′N	53°53′W	0.3
Pine Hill	55	48°36′N	53°59′W	2.5
Yudle	85	48°26′N	54°02′W	1.6

The pH was measured at the time of sampling with a Hellige pocket comparator, glass disc type, using bromthymol blue-D and bromcresol purple-D indicators. The pH was measured again titrimetrically in the laboratory just before the alkalinity determinations. Care was taken to prevent samples from coming in contact with air prior to pH determinations. Total inorganic carbon available for photosynthesis was determined from total alkalinity values, pH, and temperature from the table of Bechmann (Saunders et al. 1962).

Concentration of dissolved oxygen was measured by the azide modification of the Winkler method (Am. Public Health Assoc. 1965).

Water temperatures were measured with a calibrated thermistor thermometer with a waterproof probe on a 30-m cable, between April 28 and August 20, 1969. Before and after these dates, water temperatures were taken with a mercury thermometer with 0.1 C divisions from water samples immediately after they were brought into the boat. The heat budgets for the study lakes for the year of 1969 were calculated according to the procedure of Ruttner (1953). Correction for the latent heat of melting ice (70 cal/cm^2 per cm ice thickness) was added to the winter heat income as suggested by Hutchinson (1957). The heat required in heating the ice from its lowest temperature to 0 C was not included in the heat budget calculations because the majority of workers omitted this correction according to Hutchinson (1957).

Specific conductance was determined at 25.0 ± 1 C with a Radiometer CDM2 conductivity meter. A calibrated, direct reading Hach turbidity meter Model 1860 was employed for turbidity determinations. Apparent water color was estimated from unfiltered, uncentrifuged samples with a visual comparator equipped with 200 mm standard depth Nessler tubes (Welch 1948).

All determinations of concentrations of nutrients were made on duplicate samples. The samples were filtered through 47 mm HA Millipore filters and stored at −18 C in polyethylene containers until analysis (Golterman and Clymo 1969). Vacuum applied to the filtration assembly was kept below 380 mm Hg.

Nitrate was determined absorptiometrically as the sum of nitrate and nitrite, by reducing nitrate to nitrite (Strickland and Parsons 1968).

Duplicate samples for total dissolved phosphate were filtered and stored as described for nitrate samples, and concentrations were measured by the persulfate oxidation method (Menzel and Corwin 1965). A spectrophotometer with a 100-mm cell was used for the phosphate determinations.

Unfiltered duplicate samples of lake water for total phosphorus determination were stored frozen and the concentration was measured by the method of Menzel and Corwin (1965). Particulate phosphorus was calculated as the difference between the total phosphorus concentration of the filtered and unfiltered samples.

Chlorophyll *a* and pheophytin were determined by the fluorometric method (Yentsch and Menzel 1963; Strickland and Parsons 1968). Duplicate samples of 250 ml were filtered through 4.25 cm Whatman GF/C filters in subdued illumination. The Model 110 Turner fluorometer was calibrated against pure chlorophyll *a* extract supplied by Sigma Chemical Co., St. Louis, Missouri.

The total quantity of solar energy received on a unit area was measured with a junction pyrheliometer attached to a strip chart MV recorder. The pyrheliometer was installed on the roof of a one-story building 100 m from the field laboratory.

Underwater light intensities were measured near 1200 h using a submersible photometer supplied by the International Agency for ^{14}C Determination, Denmark, with a 48 DO1 GKA galvanometer and a selenium cell. No deck cell was used, and because maximum sampling depths were not deeper than 9 m, the instrument could be brought to the surface for immediate surface readings. The unit was equipped with a Schott VG 9 (green) filter. A 20-cm Secchi disc was also used from the shaded side of the boat. Percentage light transmissions for a series of depths were plotted on semilogarithmic coordinates, a straight line drawn through these points by inspection and the vertical extinction coefficient was calculated (Vollenweider 1969).

Maps were prepared from aerial photographs and topographical maps made by the Surveys and Mapping Branch, Canada Department of Energy, Mines and Resources. Soundings were made with electronic depth recorders.

Radiocarbon procedures are outlined in detail by Kerekes (1972, 1974b). Samples were incubated in special in situ apparatus (Watt 1965) for 3 h from 1030, suspended at 0, 0.1, 0.5, 1, 2, 3, 4, 5, 7, and 9 m depths. After incubation, measured subsamples of 25–40 ml from each bottle were filtered through 24 mm HA Millipore filters, using vacuum below 300 mm Hg to reduce the rupture of fragile algal cells (Arthur and Rigler 1967). The filters then were placed on aluminum planchettes and the activity of the filters was determined with a gasflow Geiger–Müller counter, having a micromil window. The production value of the incubation periods was expanded to the daily production value from the total photoperiod of daily pyrheliometer curves.

Kerekes (1974a) reviewed and defined the various units of primary production used by various authors. Only the following units of carbon assimilation are used in this paper:

a. *Unit volume maximum primary production* (P-max) when distinct production optimum exists on the 14 C production graphic curve, "mg C per m^3 max/time." Curves with maximum primary production at the surface, usually associated with low light intensities, are not considered (Rodhe 1958).

b. *Unit surface area primary production* (P-area) where the rates of carbon assimilation of unit volume at different depths (mg C/m^3 per time at depth *z*) are integrated for a water column in the euphotic zone "mg C per m^2/time" (Steeman Nielson 1952, 1958).

The basic statistics for the various units of primary production are calculated from values of measurements taken between May and October, 1969, and May and August, 1970, whereas other measurements are calculated from mean monthly values covering the 8-mo period between May and December, 1969. The range of values are taken from individual measurements from the same period. The coefficient of variation is used only as an index to indicate variability among lakes.

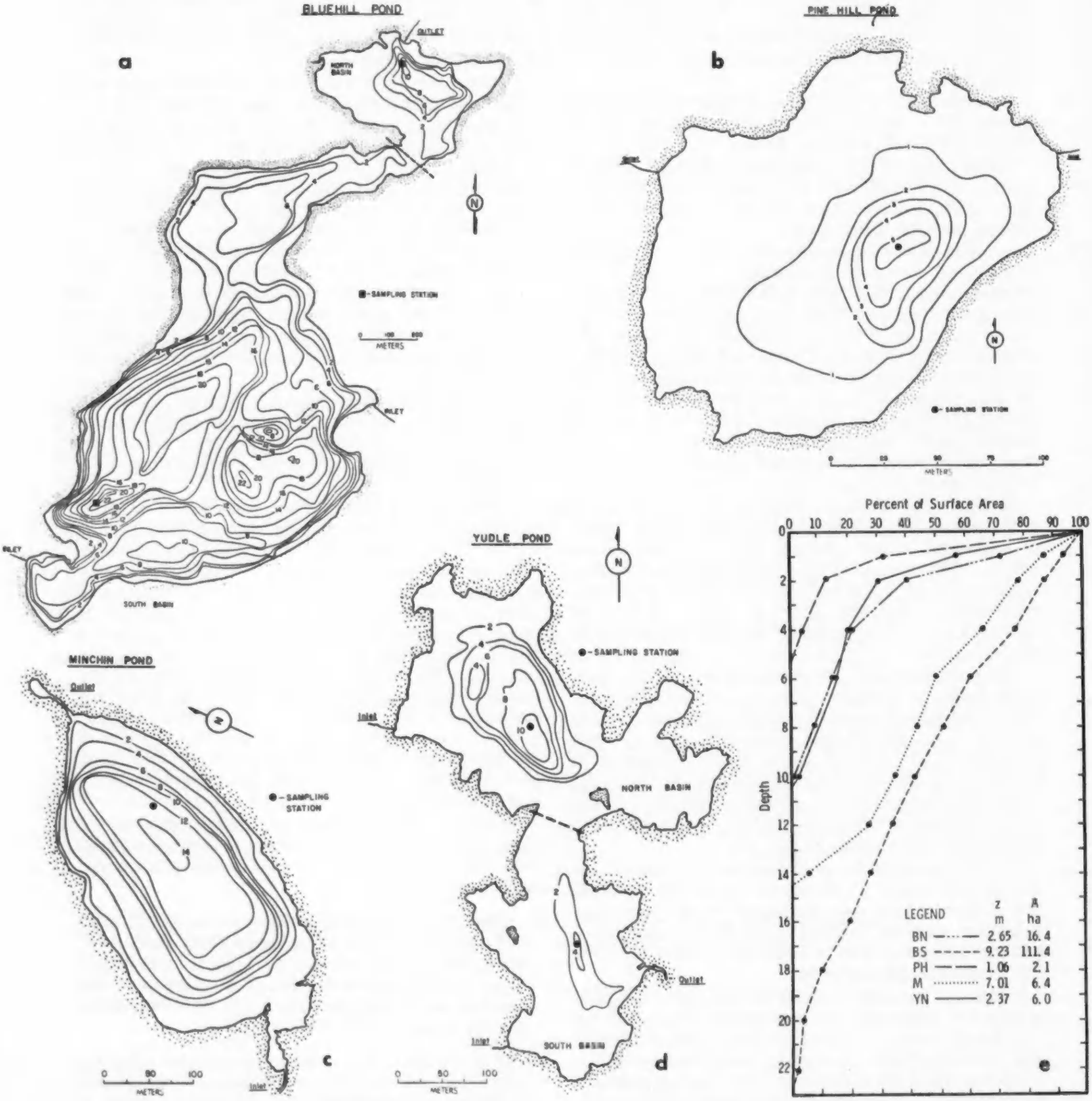

BLUEHILL POND
a
OUTLET
NORTH BASIN
INLET
SOUTH BASIN
■ - SAMPLING STATION
METERS
PINE HILL POND
b
● - SAMPLING STATION
METERS
MINCHIN POND
Outlet
● - SAMPLING STATION
c
YUDLE POND
● - SAMPLING STATION
Inlet
NORTH BASIN
SOUTH BASIN
Outlet
d
Percent of Surface Area
Depth
LEGEND
BN 2.65 16.4
BS 9.23 111.4
PH 1.06 2.1
M 7.01 6.4
YN 2.37 6.0
e

FIG. 1. a–d, Bathymetric charts for four lakes in Terra Nova National Park, Nfld. Arbitrary separation of North and South basins in Bluehill and Yudle ponds is indicated on maps by a heavy, broken line; e, hysographic curves. Abbreviations for legend are given in Table 1. Depth given in meters.

Results

Bluehill and Yudle ponds are multibasin lakes connected by narrow and shallow channels less than 1 m in depth, while Pine Hill and Minchin ponds consist of single basins (Fig. 1). Bluehill South Basin and Bluehill North Basin are treated as two separate lakes, while for Yudle only the North Basin is considered in this study. The separate basins are referred to as Bluehill North, Bluehill South, and Yudle North (Tables 2, 3). The lake drainage basins and water levels are described by Kerekes (1973a).

TEMPERATURE

Ice-cover formed in early December in 1968 (Fig. 2), beginning first on Pine Hill and ending on Bluehill South. In the following winter, surface freezing of both lakes occurred Jan. 2, 1970. The ice reached a maximum average thickness in early March, being 0.41 m in 1969 and 0.35 m in 1970. The breakup is normally in late April in the study area.

A large portion of the basins of Bluehill South, Minchin, and Yudle are of sufficient depth and shape to permit the formation of a hypolimnion and typical dimictic circulation. A hypolimnion is completely lacking in Bluehill North and Pine Hill, but summer thermoclines develop at the deepest parts of these lakes, restricted to less than 2 and 5% of total lake volume, respectively. Gradual warming of water and frequent winds during vernal circulation delayed the formation of lasting thermoclines until early June in both years. Consequently, the bottom temperatures at the deepest point were between 7 and 11 C in July 1969. Similar but somewhat higher bottom temperatures were observed in the following year.

The decline in temperature is characteristically steep in the thermocline in all lakes. In the region of the most rapid decrease in temperature, a decline of 5.0–5.5 C/m is quite common in these lakes with the exception of Bluehill North, where the greatest change of 4 C/m was recorded. In Pine Hill, temperature difference of 7.6 C between 2 and 3 m were measured June 25, 1969. Surface

TABLE 2. List of selected morphometric features of six lakes in Terra Nova National Park, Nfld; (Yudle North island area = 0.023 ha; Yudle South island area = 0.009 ha).

Pond	Abbreviation	A[a]	A′[a]	$\bar{z}$[a]	zm[a]	zc[a]	V[a]	L[a]	MEL[a]	MEW[a]
Bluehill North	BN	16.40	512.2	2.65	10.5	–	433.5	1.95	0.66	0.45
Bluehill South	BS	111.40	411.4	9.23	22.6	–	10282.5	5.98	1.94	1.04
Minchin	M	6.41	1665.0	7.01	14.5	5.5	449.5	1.01	0.38	0.20
Pine Hill	PH	2.05	19.6	1.06	5.5	–	21.8	0.71	0.21	0.16
Yudle North	YN	5.97	59.4	2.37	11.5	–	141.5	1.58	0.40	0.23
Yudle South	YS	3.63	103.5	0.97	4.6	–	35.0	0.98	0.30	0.18

[a] Abbreviations: A, area of lake (ha); A′, area of drainage basin (including lake) (ha); $\bar{z}$, mean depth (m); zm, maximum depth (m); zc, cryptodepression depth (m); V, volume of lake $m^3 \times 10^3$; L, shore length (km); MEL, maximum effective length (km); MEW, maximum effective width (km).

[b] Including island.

TABLE 3. List of morphometric indices of six lakes in Newfoundland. Abbreviations for morphometric features and their units are given in Table 2.

Pond	A″:A[a]	A″:V	WR[a]	D_L[a]	L:A[b]	(L:A):$\bar{z}$	A:$\bar{z}$	$\bar{z}$:z_m
Bluehill North	30.2	11.8	6.6	1.4	12.2	4.7	6.3	.25
Bluehill South	2.7	0.4	0.2	1.6	5.4	0.6	12.0	.41
Minchin	258.8	37.0	20.7	1.1	15.0	2.1	0.9	.48
Pine Hill	8.6	9.0	4.4	1.4	34.0	32.1	1.9	.19
Yudle North	8.9	4.2	2.4	1.8	26.0	11.0	2.5	.21
Yudle South	27.5	31.4	16.6	1.4	26.0	26.8	3.7	.21

[a] Abbreviations: A, area of lake (ha); A″, area of drainage basin, excluding lake (ha); A″:A, relative drainage basin; WR, water renewal, times per annum (water renewal coefficient); D_L, shore development including islands.

[b] Area in km^2.

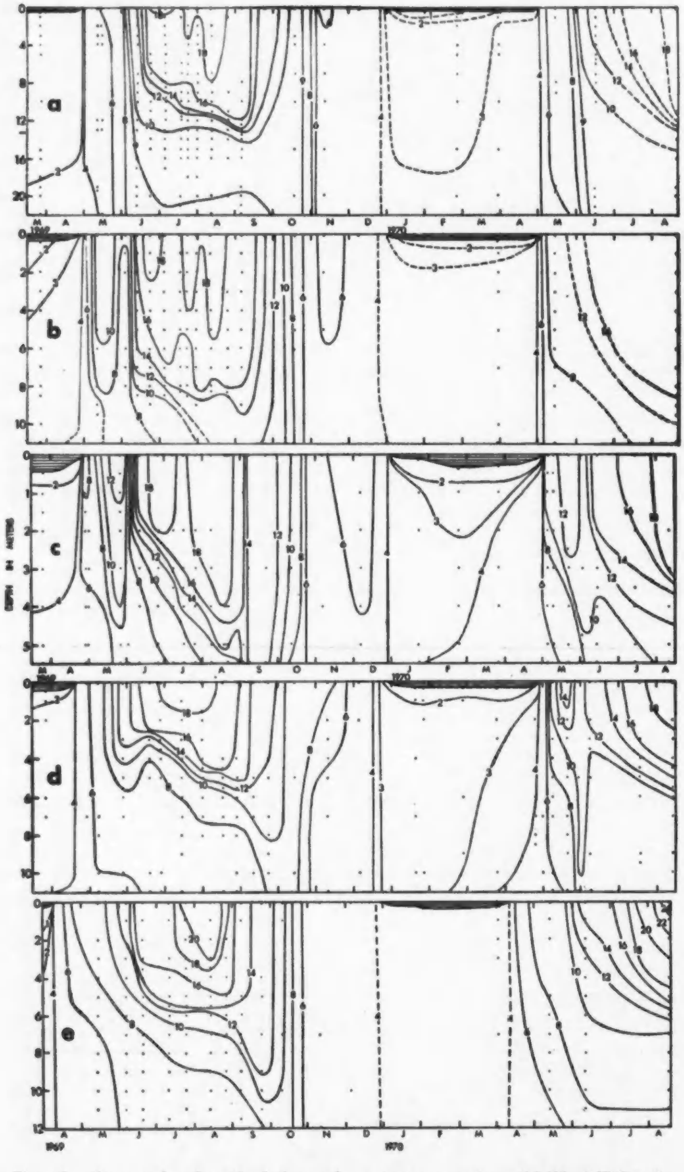


FIG. 2. Seasonal and vertical change in water temperature: (a) Bluehill South; (b) Bluehill North; (c) Pine Hill; (d) Yudle North; (e) Minchin ponds in Newfoundland in 1969 and 1970. Isopleths of temperatures in Centigrade are based on samples at each point.

TABLE 4. Heat budgets of six lakes in Newfoundland in 1968–69 in cal/cm.^{2}

Pond	Ⓗ bi[a]	Ⓗ bw[a]	Ⓗ bs[a]	Ⓗ ba[a]	Ⓗ bs/$\bar{z}$[a]
Bluehill North	2520	3380	4060	7440	1550
Bluehill South[b]	2520	5210	11770	16980	1270
Pine Hill	2840	3090	1800	4890	1698
Minchin[b]	2320	4090	7860	11950	1121
Yudle North[b]	2840	3470	2870	6340	1210
Yudle South	2840	3155	1520	4675	1567

[a] Abbreviations: Ⓗ bi, latent heat required for ice melting; Ⓗ bw, winter heat income; Ⓗ bs, summer heat income; Ⓗ ba, annual heat budget; Ⓗ bs/$\bar{z}$, summer heat income divided by mean depth (in meters).

[b] Hypolimnion present.

temperatures exceeding 21 C were observed only in Minchin in both years. In 1969, thermal stratification disappeared in all lakes in late September and the water remained in circulation with gradual cooling to a level somewhat below 4 C just prior to freezing. Increasing inverse stratification prevailed in the five lakes under the ice-cover as a result of surface heat loss and heating from the sediments, which was most rapid in the shallow Pine Hill, where water temperature as high as 4.6 C was recorded at 3-m deep March 26, 1970. A substantial increase in salinity was noted at the same time.

HEAT BUDGET

The heat budgets for 1969 are presented in Table 4. Corrections in heat budget were not made for the heat absorbed by the sediments during the summer and its subsequent loss to the water in the winter. It is clear from the regression of summer heat income and annual heat budget on mean depth in the study lakes (Fig. 3) that the deeper lakes have higher heat budgets. However, this regression is of limited value because it combines lakes with and without hypolimnial formation. The differences between these two types of lakes becomes obvious when the summer heat income is expressed as cal/cm^2 divided by mean depth (Table 4). The calculated amount of heat absorbed per meter depth during the summer in several lakes in Terra Nova National Park has a mean value of 1200 cal/cm^2 per m in lakes with a hypolimnion, and a 33% higher mean value of 1605 cal/cm^2 per m in lakes without hypolimnion. There is no overlap between the two types of lakes.

DISSOLVED OXYGEN

Isopleths in percentage air-saturation are given in Fig. 4 for the five lakes. The surface waters were usually between 95 and 105% of air-saturation for dissolved oxygen. Oxygen supersaturation (over 105%) was virtually absent in the study lakes, but epilimnetic values near 90% air-saturation and

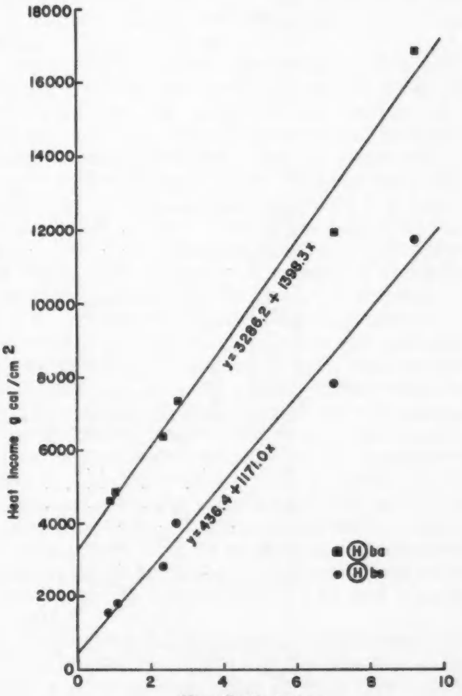


FIG. 3. Two regression lines showing the relationship between the annual heat budget (Ⓗ ba) in 1968–69, the summer heat income (Ⓗ bs) in 1969 and mean depth in six lakes in Newfoundland.

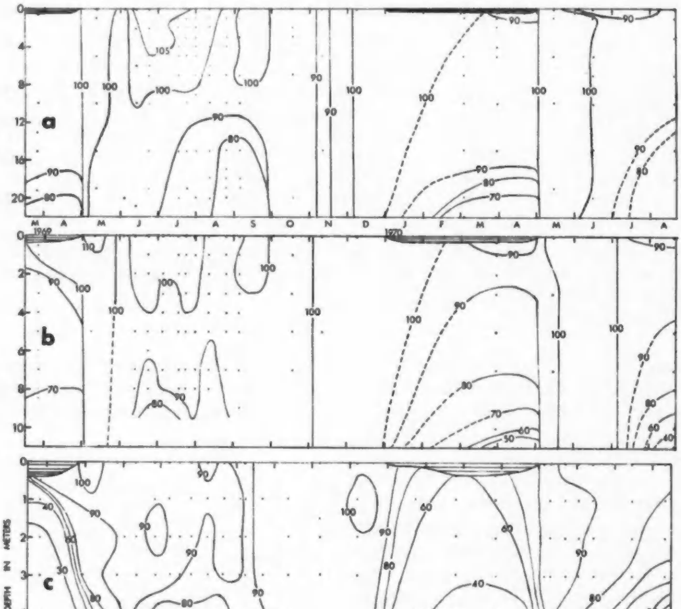


FIG. 4. Seasonal and vertical changes in dissolved oxygen: (a) Bluehill South; (b) Bluehill North; (c) Pine Hill; (d) Yudle North; (e) Minchin ponds in Newfoundland, in 1969 and 1970. Isopleths in percentage air-saturation are based on samples at each point.

lower were frequently observed, particularly in the more colored lakes.

The study lakes, with the exception of Pine Hill which is well sheltered and receives additional salts from winter road maintenance, undergo complete mixing during vernal circulation immediately after breakup. In Pine Hill a week after breakup, on April 30, 1969, the oxygen was 40% of air saturation at 4 m and 25% at 5 m depth, indicating incomplete mixing in the deepest layers which consist of only an insignificant part of the total lake volume (Fig. 1). Almost a month later, May 26, dissolved oxygen was still only 69% at 5 m. However, on June 2 the lake was isothermal at 7.9 C and dissolved oxygen was 92% from surface to bottom at the deepest point, indicating mixing was complete. At the end of the period of summer stagnation the level of oxygen was still over 10% at 5 m. In 1970, only partial mixing took place below 5 m during vernal circulation. The highest levels of oxygen, 49% at 5 m and 44% at 5.5 m at the bottom, were measured June 14. Only a trace of oxygen was present at 5 m and it was completely absent at the bottom on a foggy, rainy Aug. 11. On Aug. 26, the level of oxygen increased to 3% at 5 m and traces of oxygen were found at the bottom. The increase in oxygen concentration was probably caused by photosynthetic activity of the greatly accumulated algae at that depth responding to increased transmitted solar isolation. The rate of primary production was an order of magnitude higher at 5 m on the latter day.

The vertical distribution of oxygen concentration was almost orthograde in Bluehill South and clinograde in the other four lakes at the end of summer stagnation in both years. With the exception of Pine Hill, mentioned previously, complete oxygen depletion did not take place in the study lakes during summer stagnation. Oxygen levels less than 10% were found in Yudle North, near 30% in Minchin, and over 70% in Bluehill South at the deepest point near the mud surface at the end of August in both years. The average oxygen concentration per unit volume in the hypolimnion remained relatively high at 5.1 mg/liter (Aug. 13, 1970), 7.1 mg/liter (Aug. 17, 1970), and 8.6 mg/liter (Aug. 25, 1969), respectively, in the three lakes in late summer. Oxygen levels under the ice in March 1970 were similar to those at the end of the summer stagnation.

OXYGEN DEFICIT

The relative hypolimnetic oxygen deficits (Hutchinson 1938) were calculated for the three lakes where hypolimnions developed. The rates of oxygen deficits thus obtained were 111 mg O_2/m^2 per day for Bluehill South, 224 mg O_2/m^2 per day for Minchin, and 217 mg O_2/m^2 per day for Yudle North after 63, 69, and 67 days of summer stagnation, respectively. The corresponding hypolimnetic oxygen deficits per unit volume were 32, 43, and 98 mg O_2/m^3 per day.

WATER COLOR

Water color was consistently higher in all lakes during the more rainy summer of 1970 than in 1969 (Fig. 5, 6).

Marked seasonal, vertical, and annual variation of water color was observed in Pine Hill. The highest values during the ice-free period were recorded shortly after heavy rainfalls such as it was observed in June 1969, when color increased from 20 Hazen units on May 26 to 50 units by June 10 after heavy rainfalls. The lowest value of 15 Hazen units was recorded in September 1969. In late August, at 5 m, color reached 80 units in both years and in 1970 it exceeded 120 units near the bottom (5.4 m). Three months earlier, on May 4, 1970, water color was 10 units at 5 m, the lowest value recorded in Pine Hill.

Water color changes at 1 m followed a well-defined seasonal pattern in Yudle North, where it was relatively high after the ice breakup, decreased gradually during the summer, increased again until the ice formed, then the highest values were recorded shortly after ice formation. The color for the 8-mo standard period at 1 m had a mean value of 38.1 Hazen units with a 33.3% coefficient of variation, the greatest seasonal change in the five lakes (Table 5). Color values at all depths reached 50 units after breakup in both years in 1969 and 1970. The lowest values (20 units) at 1 m was measured in August 1969, which increased to 55 units in December and 80 units under the ice in January. Water color reached higher values in the hypolimnion in both summers, as compared to the epilimnion. Water which was trapped below the thermocline in early summer was considerably more colored than that in the epilimnion and it continued to increase in the hypolimnion as summer progressed. The result was a marked vertical change in color distribution, an example of which was the observation of September 9, 1969, when water color was 25 units at 1 m, 45 units at 7 m, and 70 units at 10 m.

The least amount of seasonal and annual variation in water color at 1 m was found in Minchin, which had a mean monthly value of 43.8 Hazen units with a coefficient of variation of 7.5% between May and December 1969. Noticeable increase in color with increase in depth was observed only at 12 m at the end of summer stagnation, when 70 units was measured in September 1969.

The least colored water was found in Bluehill South. Vertical gradation in color was virtually absent during the summer stagnation.

Considerable vertical, seasonal, and annual variation in water color was observed in Bluehill North. Vertical variation was absent during the

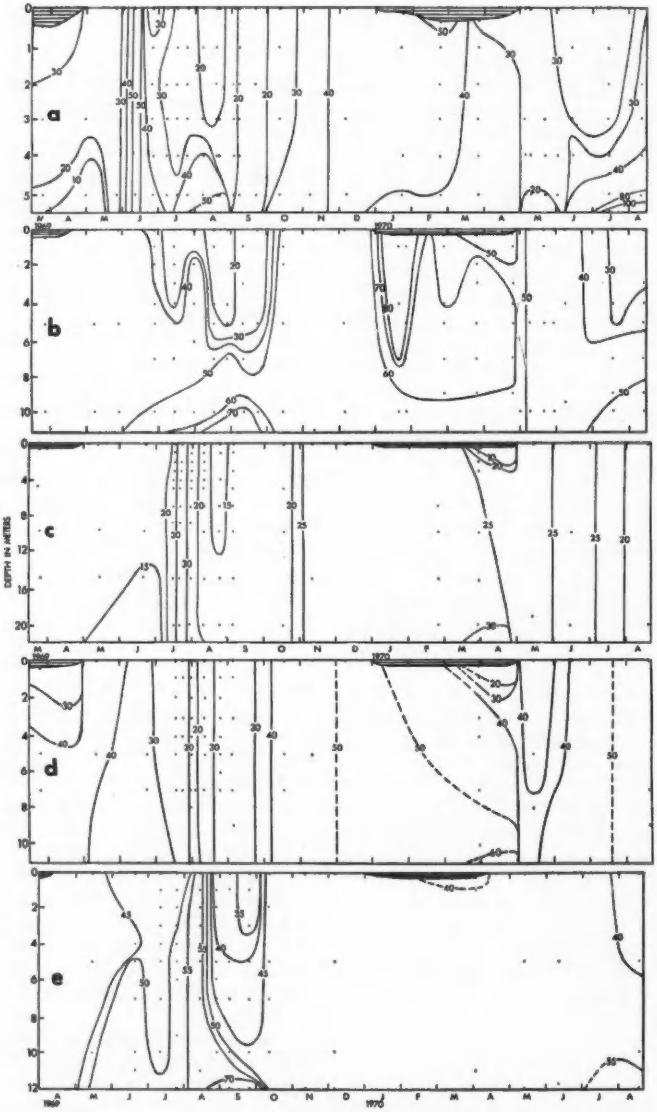


FIG. 5. Seasonal and vertical changes in water color: (a) Bluehill South; (b) Bluehill North; (c) Pine Hill; (d) Yudle; (e) Minchin ponds in Newfoundland, in 1969 and 1970. Isopleths in Hazen units are based on samples at each point.

ice-free period in both years. On March 31, 1970, color increased markedly with increase in depth from 15 Hazen units just below the ice (0.3 m) to 40 units at 2 m and 60 units at 11.4 m.

TURBIDITY

The lowest turbidities, not exceeding 0.2 Jackson units, were found in Bluehill North and Bluehill South. Epilimnetic turbidity values were usually in the range of 0.1–0.3 units in the other three lakes, but occasionally higher turbidities, not exceeding 0.9 units, were measured in these. Turbidity was frequently in the range of 1.0–3.0 units in Pine Hill at 5 m during the summer thermal stratification. The increase in turbidity was usually associated with a similar increase of phytoplankton standing stock, indicated by chlorophyll *a* concentrations.

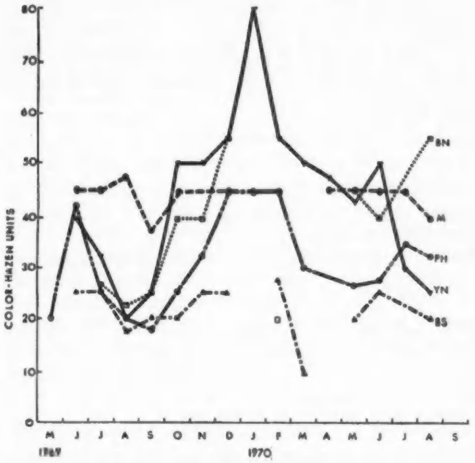


FIG. 6. Mean monthly values of water color (Hazen units) at 1 m depth in Bluehill North (BN), Bluehill South (BS), Pine Hill (PH), Minchin (M), and Yudle North (YN) ponds in Newfoundland, between April 1969 and August 1970.

TABLE 5. The monthly mean and the range of values of water color at 1 m, as found in the five lakes studied in Newfoundland, from May to December 1969. The coefficient of variation (C.V.) is used in this case as an index to indicate variability among lakes.

Pond	Hazen units		C.V.(%)
	Mean	Range	
Bluehill North	34.8	20–55	31.9
Bluehill South	22.1	15–30	13.7
Minchin	43.8	35–55	7.5
Pine Hill	29.4	15–55	30.4
Yudle North	38.1	20–55	33.4

TRANSPARENCY

The highest Secchi disc transparency (6.7 m) and the lowest average vertical light extinction coefficient (0.3), during the ice-free study period, occurred in Bluehill South, which had the least colored water (Tables 6, 7); the lowest transparencies were measured in Minchin and Yudle North, 3.4 and 3.5 m, respectively, for the same period. The highest vertical light extinction coefficient for green light (1.61), during the ice-free period, occurred in Yudle North in December 1969 (Fig. 7). The seasonal variation in transparency was the greatest in Yudle North Pond among the five lakes.

During the period of summer thermal stratification, when highly colored water was trapped

TABLE 6. The monthly mean and range of Secchi disc readings as found in five lakes studied in Newfoundland from May to December, 1969. The coefficient of variation (C.V.) is used in this case as an index to indicate variability among lakes.

Pond	meters		C.V.(%)
	Mean	Range	
Bluehill North[a]	4.70	3.8–5.6	11.8
Bluehill South[b]	5.90	5.0–6.7	9.5
Minchin	4.21	3.4–4.6	7.7
Pine Hill	4.33	3.6–5.0	9.0
Yudle North	4.24	3.5–5.9	20.1

[a] Between June and November.
[b] Between June and December.

TABLE 7. The monthly mean and range of light extinction coefficients as found in five lakes studied in Newfoundland from May to December 1969. The coefficient of variation is used in this case as an index to indicate variability among lakes.

Pond	Mean	Range	C.V.(%)
Bluehill North	0.703	0.40–1.59	43.5
Bluehill South	0.481	0.29–0.65	23.6
Minchin	0.959	0.79–1.22	18.8
Pine Hill	0.763	0.37–1.31	43.3
Yudle North	0.914	0.35–1.61	51.0

below the thermocline, the vertical light extinction increased sharply with increases in depth, in and below the zone of thermocline in Bluehill North, Pine Hill, and Yudle North.

WATER CHEMISTRY

Major ions — The concentrations of each of the major ions, Na^{++}, K^{+}, Ca^{++}, Mg^{++}, HCO_3^-, Cl^-, $SO_4^=$ were very low in the study lakes, thus analytical error often exceeded seasonal variation in ion concentrations. Therefore, to remove inaccuracies caused by analytical error, the analytical values of one sample per month, taken from the water surface, were averaged for the period of April–December, 1969 (Table 8). The average values of water samples taken at near maximum depth in each lake for this period were virtually identical to the respective values obtained from the surface samples. The difference of the sum of cations less the sum of anions over total ions of the averaged ionic constituents was in the range of 0.2–1.7%, which was within the limits of acceptability given by Thomas (1953).

The highest mean salinity of 42.9 mg/liter occurred in Pine Hill, while in the other four lakes mean salinities were in the range of 18.2–21.4 mg/liter, and Minchin had the lowest value.

The cationic order of dominance on a molar basis was Na > Ca > Mg > K in Minchin, and Ca > Na > Mg > K in the remaining four lakes, where the position of calcium and sodium was reversed by only a small margin and they were virtually equal in Pine Hill. The anionic order of dominance was $Cl > HCO_3 > SO_4$ in all lakes.

The ratio of total alkalinity to specific conductance ranged from 0.22 (Minchin) to 0.33 (Yudle) and the ratio of salinity to specific conductance from 0.51 (Pine Hill) to 0.62 (Bluehill North) in the five lakes.

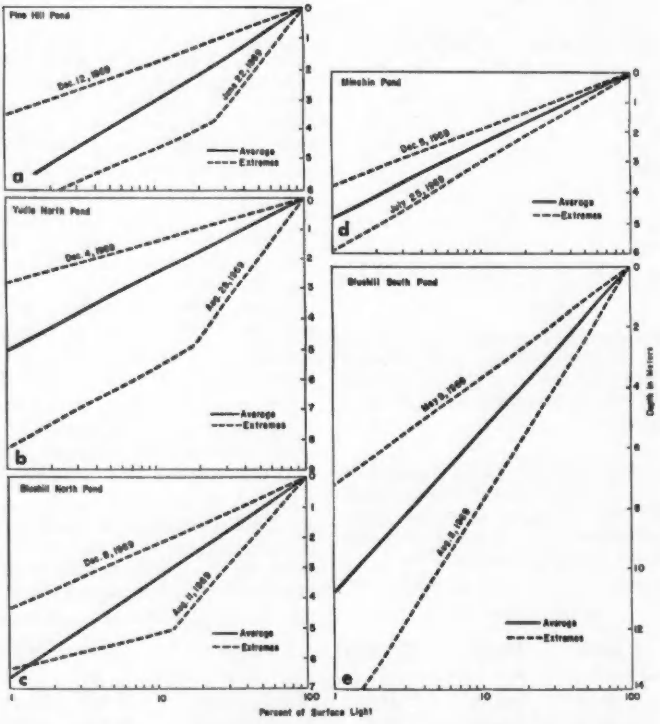


FIG. 7. Average vertical attenuation of green light indicated by solid line between May and December, 1969: (a) Pine Hill; (b) Yudle North; (c) Bluehill North; (d) Minchin; (e) Bluehill South ponds in Newfoundland. Broken lines indicate the range of attenuation for the same period.

Table 8. Average concentrations of major ions, reactive silica, and salinity (mg/liter) from the water surface, based on monthly samples between April and December 1969 in the five lakes studied in Newfoundland.

Pond	Ions, mg/liter								
	Ca^{++}	Mg^{++}	Na^{+}	K^{+}	NCO_3^-	$SO_4^=$	Cl^-	SiO_2	Salinity
Bluehill North	3.0	0.7	2.9	0.5	6.6	4.2	4.9	2.2	21.4
Bluehill South	2.8	0.5	2.9	0.6	6.9	3.2	4.9	2.2	20.3
Pine Hill	6.2	1.3	6.9	1.1	13.0	5.7	14.0	1.1	42.6
Minchin	1.9	0.6	2.9	0.4	4.9	3.0	5.0	2.0	18.2
Yudle North	3.3	0.5	2.8	0.4	7.9	2.9	4.8	1.2	19.8

Marked increase in salinity occurred in Pine Hill at 5 m and a modest increase occurred at 10 m in Yudle North under the ice, where salinities increased to 133.7 mg/liter on March 26, 1970 in Pine Hill and to 25.0 mg/liter on March 25, 1970 in Yudle North. The respective increases in salinity were somewhat higher in the two lakes in March 1969, when higher quantities of salt were used in winter road maintenance. Substantial increases in Na^{++} and Cl^- concentrations were mainly responsible for salinity increases, while Na^{++}, Mg^{++}, HCO_3^-, and $SO_4^=$ concentrations increased only moderately and K^+ concentrations remained unchanged compared to the summer concentrations. The concentration of Cl^- alone, 94.0 mg/liter in March 1969, and 55.0 mg/liter at 5 m in March 1970 was greater than the average salinity in the ice-free period in Pine Hill.

SPECIFIC CONDUCTANCE

Spring and summer values of specific conductance were higher in 1969 than in 1970 (Fig. 8, 9). Seasonal trends in specific conductance at 1 m followed a similar pattern in four lakes during the ice-free period, values being lowest after breakup, then gradually increasing until late summer and decreasing until ice formation.

In Pine Hill the lowest value in specific conductance occurred during autumn. Small seasonal, annual, and marked vertical, variation in specific conductance occurred in Pine Hill. Specific conductance began to increase at all depths after the formation of the ice, resulting in an inverse clinograde distribution and it reached 106 μmho at 1 m and 300 μmho at 5 m. Subsequently, when meltwater entered the lake it declined to 78 μmho at 1 m by March 16, 1969, but it continued to increase below 2 m until breakup. The highest value of 560 μmho at 5 m occurred after breakup on May 5, 1970 when 83 and 98 μmho were measured at the surface and at 3 m, respectively. Specific conductance remained fairly high at 5 m until June 2, 1970, but it decreased to 99 μmho on June 14, 1970, with corresponding values of 85 and 87 μmho at 1 and 5 m respectively. Strong inverse clinograde distribution in specific conductance was noted in both summers.

Seasonal variation in specific conductance at 1 m was greatest in Yudle North among the five lakes. The lowest value of 29.0 μmho at 1 m occurred on April 29, 1969 shortly after breakup and on June 8, 1970, preceded by 33 mm rain on the previous 6 days, and the highest value, 40.0 μmho occurred on Sept. 9, 1969. Specific conductance showed a negative heterograde distribution with minimum value at 7 m during summer stagnation in 1969 and 1970.

Early winter values at all depths were in the range of 30–35.5 μmho with highest values immediately below the ice, in January and February, 1970. Inverse clinograde distribution in specific conductance occurred under the ice on March 25 and April 24, 1970 when, on the latter date, values ranged from 19.0 to 47.1 μmho at 1 and 9 m, respectively, when strong flow of meltwater with a specific conductance of 19.1 μmho was entering the lake.

Seasonal and vertical variation in specific conductance was very small in Minchin and Bluehill. Annual variation in specific conductance was the greatest in Bluehill North among the five lakes.

HYDROGEN-ION CONCENTRATION

Surface pH values at 1 m were in the range of 6.2–7.1 during the ice-free period and 5.9–6.7 under the ice in the five lakes (Fig. 10). Values with corresponding dates were usually lower in 1970 than in 1969 after breakup of ice. Clinograde vertical distribution in pH occurred during the summer stagnation except in Pine Hill, where negative heterograde distribution was present on Aug. 11 and 16, 1970. The greatest vertical difference of 1.0 pH unit between surface and near bottom values occurred in Yudle North in both summers. Under the ice,

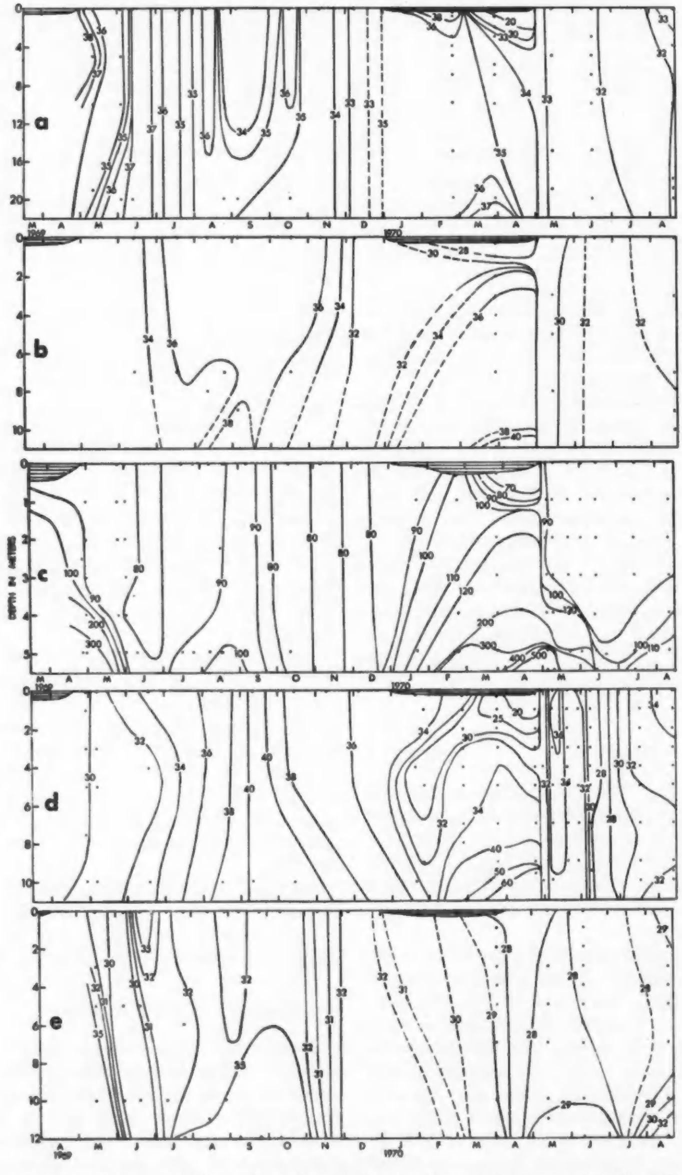


FIG. 8. Seasonal and vertical changes in specific conductance: (a) Bluehill South; (b) Bluehill North; (c) Pine Hill; (d) Yudle North; (e) Minchin Pond in Newfoundland, in 1969 and 1970. Isopleths of specific conductance in μmho/cm at 25 C are based on samples at each point.

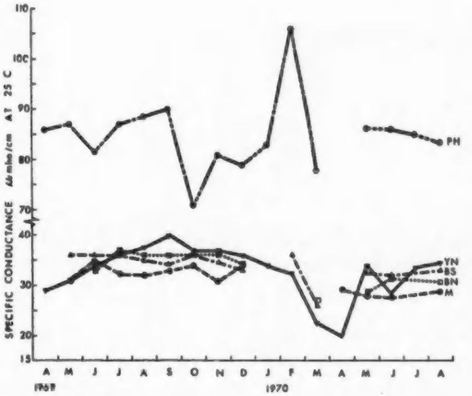


FIG. 9. Mean monthly values of specific conductance (µmho/cm at 25.0 C) at 1 m depth in Bluehill North (BN), Bluehill South (BS), Minchin (M), Pine Hill (PH), and Yudle North (YN) ponds in Newfoundland, between April 1969 and August 1970.

inverse clinograde vertical distribution in pH occurred in Pine Hill and clinograde distribution in the other lakes, except in Bluehill South which at the second winter sampling had a positive heterograde distribution on March 29, 1970.

TOTAL ALKALINITY

Spring and summer values of total alkalinity were consistently lower in 1970 than in 1969 (Fig. 11). Seasonal trends in total alkalinity at 1 m followed a similar pattern in the five lakes during the ice-free period, values being the lowest usually after breakup, then gradually increasing until late summer and then decreasing until ice formation (Fig. 12).

Noticeable seasonal, annual, and strong vertical variation of total alkalinity was found in Pine Hill, which had the highest total alkalinity values among the study lakes. Total alkalinity at 1 m was the lowest, approximately 1 mo after breakup in both years. The highest value, 11.7 mg/liter at 1 m, occurred Sept. 8, 1969. Total alkalinities under the ice-cover were comparable to that of the ice-free period. Strong vertical stratification in total alkalinity was found immediately after breakup on April 28, 1969, when measured values increased from 9.7 mg/liter at surface to 32.0 mg/liter at 4 m. Earlier, total alkalinity was 11.2 mg/liter under the ice, 26.7 mg/liter at 3 m, and 42.0 mg/liter at 5 m on March 25, 1969. After vernal circulation total alkalinity was 8.9 mg/liter at all depths on June 2, 1969. By late August of that year, it increased to 11.4 mg/liter at surface and to 15.8 mg/liter at 5 m. After the formation of the ice cover in 1970, total alkalinity values began to increase, with the highest values toward the bottom.

The seasonal variation in total alkalinity at 1 m was the greatest in Yudle North; among the five lakes it had the second highest mean monthly value of 6.79 mg/liter. Total alkalinities at 1 m under the ice were well below the summer values. Vertical stratification in total alkalinity occurred whenever thermal stratification prevailed in Yudle North, but its pattern was different to that of Pine Hill, because in Yudle North total alkalinity at the deepest part of the lake did not exceed the surface values during summer stagnation and the total alkalinity values were always lowest in the upper hypolimnion.

Total alkalinity values were the lowest in Minchin and seasonal, vertical, and annual variation in total alkalinity was the smallest in Bluehill. Values in Bluehill North were similar to that of Bluehill South, but the seasonal variation was greater.

TOTAL INORGANIC CARBON

The average value of total inorganic carbon, at 1 m, ranged from 1.5 mg/liter (Minchin) to 3.4 mg/liter (Pine Hill) in the five lakes from May to December, 1969 (Table 9). Extreme values were 1.3 mg/liter (Minchin) and 4.0 mg/liter (Pine Hill) for the same period. Seasonal variation in inorganic carbon was generally small in the five lakes.

NITRATE

Little vertical stratification of nitrate was noted during the summer months in 1969 and it was completely absent in 1970 in Pine Hill, where the euphotic zone is extended to the bottom in this period (Fig. 13). Concentrations at all depths were in the range of 0.3–2.7 µg-at N/liter during the ice-free period after the vernal circulation in both years. Noticeable vertical stratification of nitrate was present in both winters with gradual increase in concentrations with increase in depth; when at 5 m, concentrations were close to 6.0 µg-at N/liter in late March 1969 and 1970. Winter concentrations were significantly higher than those in the ice-free period.

In contrast to Pine Hill, noticeable vertical stratification of nitrate occurred in Yudle North during summer stagnation in both summers, when concentrations were in the range of 0.7–2.6 µg-at N/liter in the euphotic zone and 2.5–4.9 µg-at N/liter in the aphotic zone. Spring and autumn concentrations at all depths fell within the range of concentrations measured in the euphotic zone during summer stagnation.

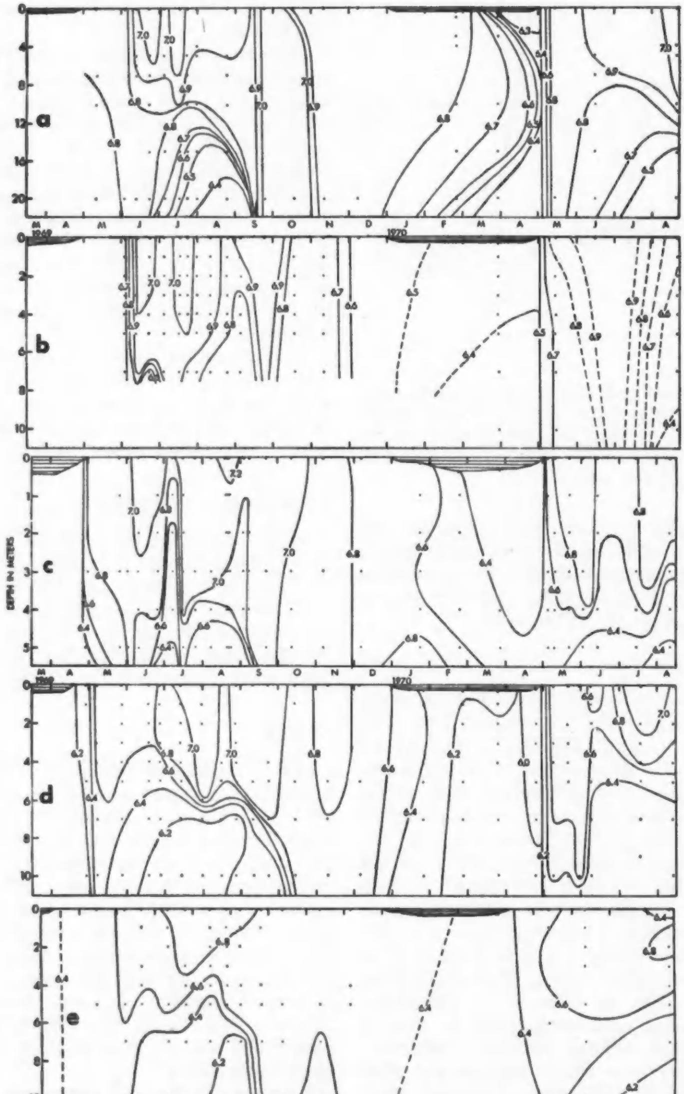


FIG. 10. Seasonal and vertical changes in pH; (a) Bluehill South; (b) Bluehill North; (c) Pine Hill; (d) Yudle North; (e) Minchin ponds in Newfoundland, in 1969 and 1970. Isopleths of pH are based on samples at each point.

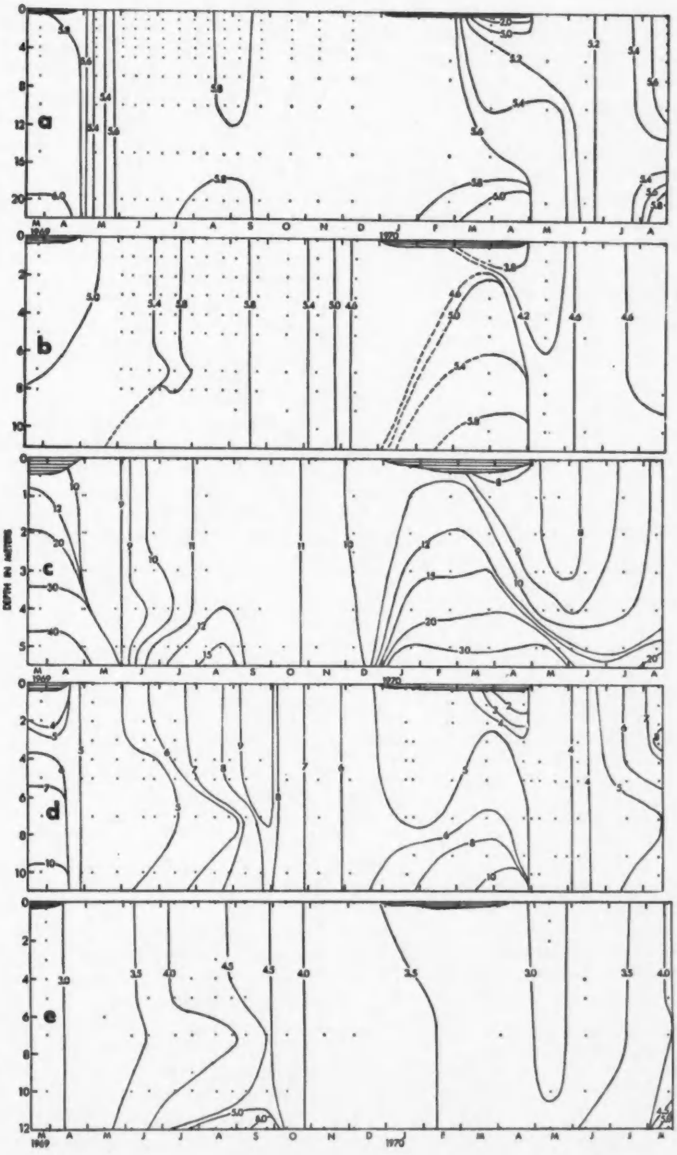


Fig. 11. Seasonal and vertical changes in total alkalinity concentration: (a) Bluehill South; (b) Bluehill North; (c) Pine Hill; (d) Yudle North; (e) Minchin ponds in Newfoundland, in 1969 and 1970. Isopleths of total alkalinity in $CaCO_3$ mg/l areiter based on samples at each point.

Vertical stratification of nitrate in Minchin during the summer stagnation showed the same general pattern found in Yudle North where concentrations in the euphotic zone were less than those in the aphotic zone. Some seasonal trend was recognizable when concentrations in the epilimnion, which was entirely within the euphotic zone, did not exceed 1.9 μg-at N/liter in the two summers, whereas concentrations between October and December, 1969 were greater than 2.2 μg-at N/liter.

Vertical stratification of nitrate in Bluehill South during the summer stagnation showed the same general pattern described in Yudle North and Minchin, while little vertical stratification of nitrate was noted in Bluehill North.

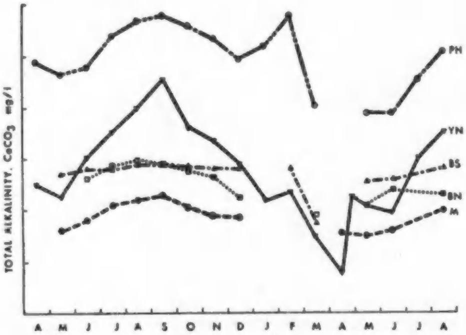


FIG. 12. Mean monthly values of total alkalinity ($CaCO_3$, mg/liter at 1 m depth in Bluehill North (BN), Bluehill South (BS), Minchin (M), Pine Hill (PH), and Yudle North (YN) ponds in Newfoundland, between April 1969 and August 1970.

TABLE 9. The monthly mean and the range of values of total available inorganic carbon at 1 m as found in the five lakes studied in Newfoundland from May to December, 1969. The coefficient of variation (C.V.) is used in this case as an index to indicate variability among lakes.

Pond	Inorganic carbon mg/m³ Mean	Inorganic carbon mg/m³ Range	C.V.
Bluehill North[a]	1834	1590–1964	4.9
Bluehill South	1878	1767–2005	4.4
Minchin	1507	1333–1687	7.0
Pine Hill	3432	2880–3959	8.7
Yudle North	2264	1764–2806	14.6

[a] Between June and November.

PHOSPHORUS

Total phosphorus concentrations in the surface water were usually in the range of 0.1–0.6 mg-at P/m³ in the five lakes between May and August, 1970. Particulate phosphorus concentrations were in the range of 0.06–0.30 mg-at P/m³ in surface waters for the same period. A total phosphorus concentration of 0.182 mg-at P/m³ was measured at the inlet of Yudle North April 30, 1970 at the time of maximum runoff. The concentration at the outlet, 0.148 mg-at P/m³, was somewhat lower on the same day. The highest concentration of total phosphorus in this study, 1.33 mg-at P/m³, of which 1.16 mg-at P/m³ was in the form particulate phosphorus, was found at the depth of 5 m in Pine Hill in August 1970. This high concentration of phosphorus coincided with an unusually high phytoplankton standing stock, indicated by the high chlorophyll *a* concentrations.

The highest concentration of total phosphorus per unit volume, representative for the whole lake, in late summer, occurred in Pine Hill (0.440 mg-at $P/m^3\bar{x}$), and the lowest concentration (0.124 mg-at $P/m^3\bar{x}$) was measured in Bluehill South (Kerekes 1973a).

CHLOROPHYLL *a*

The euphotic zone usually extended to the basin of Pine Hill except under extreme low light intensities during the ice-free period. Chlorophyll *a* concentrations at 1 m were in the range of 0.5–2.0 mg/m³ during the ice-free study period (Table 10). Concentrations of 3.0 to 6.0 mg/m³ occurred frequently in the thermocline, usually with values increasing with depth (Fig. 14). Exceptionally high concentrations of 13.6 and 57.0 mg/m³ were found at 5 m on Aug. 21, 1969 and Aug. 11, 1970, respectively. Clinograde vertical distributions in chlorophyll *a* were found Jan. 23 and Feb. 22, 1970, when the values of 1.6 and 1.4 mg/m³, respectively, under the ice were within the range of values which occurred in the ice-free period. The corresponding values at 2 m were 0.36 and 0.45 mg/m³. A positive heterograde vertical distribution was found on March 26, 1970 with concentrations of 0.47 mg/m³ under the ice and 1.9 mg/m³ at 2 m.

Concentrations at 1 m were generally the lowest in Yudle North, 0.8 mg/m³ between May and December, 1969, which was the lowest among the five lakes. Vertical distribution of chlorophyll *a* concentration usually showed a positive heterograde pattern with peak concentrations in the thermocline near 4 m. Winter concentrations were similar to those described in Pine Hill. The chlorophyll *a*

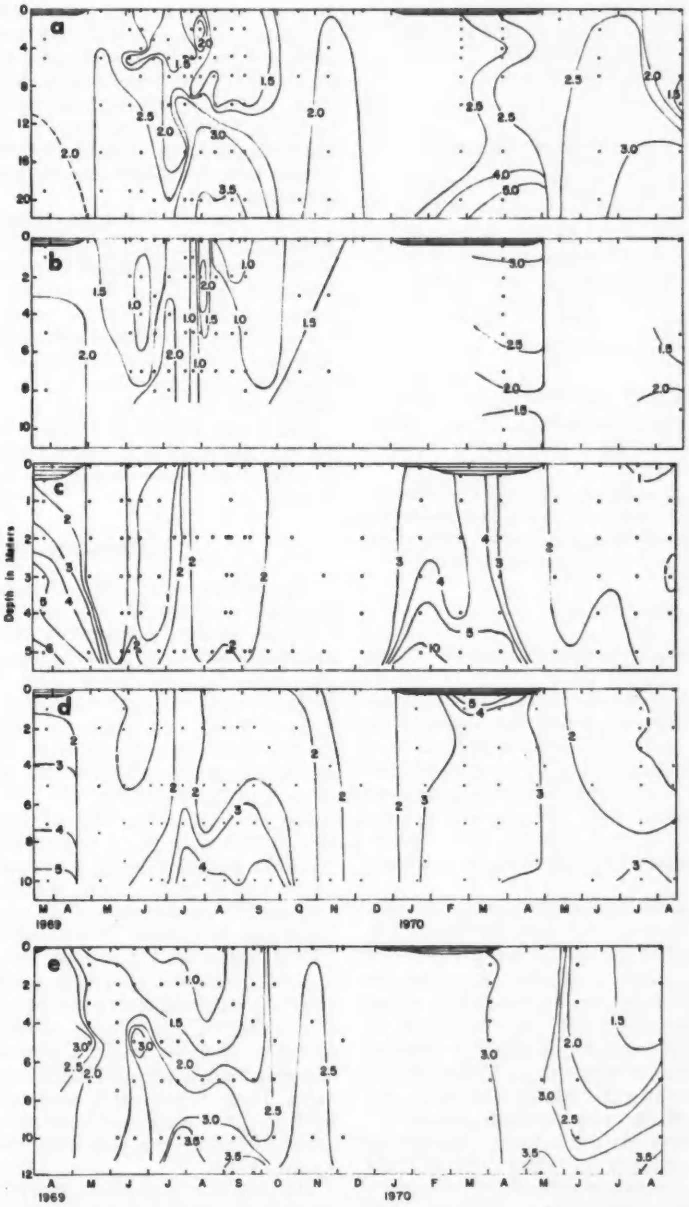


FIG. 13. Seasonal and vertical changes in nitrate concentration: (a) Bluehill South; (b) Bluehill North; (c) Pine Hill; (d) Yudle North; (e) Minchin ponds in Newfoundland in 1969 and 1970. Isopleths of nitrate μg-at N/liter are based on samples at each point.

TABLE 10. The monthly mean and the range of chlorophyll *a* concentration at 1 m depth between May and December, 1969 in the five lakes studied in Newfoundland.

Pond	Chlorophyll *a* mg/m³	
	Mean	Range
Bluehill North	1.56	1.01–2.00
Bluehill South	1.26	0.77–1.56
Pine Hill	1.41	0.77–2.00
Minchin	1.61	1.02–3.21
Yudle North	0.80	0.52–1.20

concentrations of 0.05 and 0.14 mg/m³ measured immediately under the ice and at 1 m, respectively, March 25, 1970 were the smallest values found in this study.

In the other three lakes chlorophyll *a* concentrations fell sharply below the euphotic zone during thermal stratification when the vertical distribution characteristically had a clinograde pattern.

PRIMARY PRODUCTION

The daily primary production rates for P-max and P-area are summarized in Tables 11 and 12 for the growing season during the study period. A recognizable seasonal trend, with some irregularities, was in evidence in all five lakes as production gradually increased after breakup, reached its peak in late August and early September, and gradually decreased until ice formed. Photoinhibition in surface water (Rodhe 1958; Vollenweider and Nauwerck 1961) was always in evidence on sunny days.

The highest rates of primary production were found in Pine Hill. P-max occurred between 0.5 m and 2.0 m during the ice-free season. The euphotic zone usually extended to the bottom across the basin in Pine Hill during the ice-free period, except on days with extremely low light intensities. A second production peak was frequently observed in the thermocline on bright days. Under the ice, particularly when it was covered with snow, the depth of the euphotic zone declined sharply.

P-max was always near 0.5 m depth when surface light inhibition occurred on bright days in Yudle North. Daylight compensation depths where primary production equals respiration (Goldman 1960) varied seasonally with strong positive correlation with surface light intensities and negative correlation with water color. It occurred usually near 7 m but it reached down to 9 m on bright days in August and was near 4 m when water color was high and irradiance was low. The compensation depth was only 2 m or less under the ice, except on April 24, 1970 on an exceptionally bright day when under 0.33 m ice, compensation depth was extended to 5.5 m. Carbon uptake usually fell sharply below the production maximum on the vertical production profile and diminished rapidly toward to compensation depth.

P-max was near 0.5 m, the compensation depth was estimated to be near 7 m on bright days but it was reduced to 5 and 4 m on days with low light intensities in Minchin. The carbon uptake always fell very rapidly below 3 m.

P-max was the deepest among the study lakes in Bluehill South Pond, being near 1.5 m, and its mean rate was the lowest. Daylight compensation depths were usually near 10 m on bright days.

P-max was between 0.5 and 1.0 m in Bluehill North. Daylight compensation depths reached 9 m in August, but were around 7 m or less in other months.

Discussion

The average total ionic concentrations in the five lakes are very low and are examples of the dominant effect of precipitation on chemical characteristics, Na^+ being the most abundant or nearly the most abundant cation, and Cl^- being the dominant anion (Kerekes 1973a). The concentrations of major and minor elements examined in the five lakes are well within the range of values considered to be characteristic of oligotrophic lakes (Vollenweider 1968).

The specific conductance of the five lakes is considerably higher than that of continental lakes of similar salinities on the Canadian Shield (Armstrong and Schindler 1971), owing mainly to the high specific conductance of Cl^- (Gorham 1957). Significant correlation ($P < 0.001$) exists between specific conductance and total ion concentrations ($r = 0.92$; total ions m.eq./liter $= 0.038 + 0.016x$), specific conductance and chloride concentrations ($r = 0.90$; Cl^- mg/liter $= -0.193 + 0.155x$) in 39 lakes and ponds in Terra Nova National Park, including the five lakes studied (Kerekes unpublished data). Thus, a reasonably accurate estimation of total or each ion-concentration can be made from specific conductance, following the method of Rodhe (1949).

The relatively high average salinity in Pine Hill, which is about twice that in 38 other lakes in Terra Nova National Park, is caused at least partially by the salt used for the ice removal on the Trans Canada Highway, which bisects the catchment area of Pine Hill (Kerekes 1973a).

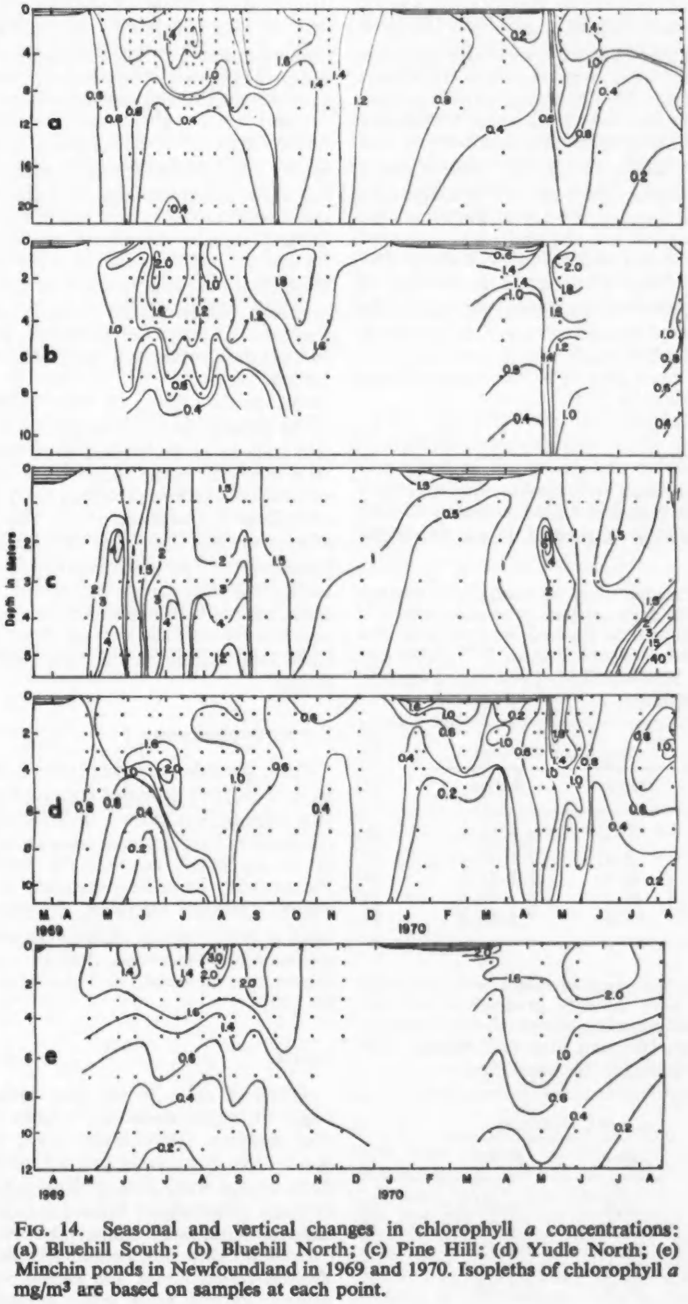


FIG. 14. Seasonal and vertical changes in chlorophyll *a* concentrations: (a) Bluehill South; (b) Bluehill North; (c) Pine Hill; (d) Yudle North; (e) Minchin ponds in Newfoundland in 1969 and 1970. Isopleths of chlorophyll *a* mg/m^3 are based on samples at each point.

Variations in runoff from precipitation caused seasonal and annual changes in salinity in the lakes as indicated by specific conductance. Salinity was lowest in the four lakes other than Pine Hill Pond during the diluting effects of spring runoff, greatest during high summer evaporation, and declining again in autumn with increasing precipitation and decreasing evaporation, in parallel with northern Swedish lakes (Rodhe 1964) and an Alaskan lake (Kalff 1967). In spite of the low salinities in the five lakes, separation of salts and water occurred by freezing in January and February, both in 1969 and 1970, and this process caused an increase in salinities restricted to a narrow layer below the ice. The amount of precipitation during the spring and summer of 1970, which was greater than that in 1969 for the same period, reduced the salinities in all of these lakes in 1970.

TOTAL ALKALINITY

Seasonal and annual variations in total alkalinity in surface waters followed a pattern similar to that described for salinity, in general, in the five lakes. The inverted clinograde distribution in total alkalinity in Pine Hill Pond during the summer stagnation was caused by the bicarbonate concentration which was initially high in deep water at the time formation of thermal stratification and its subsequent release from the sediments as the summer progressed (Hutchinson 1957). The negative heterograde distribution in total alkalinity in the other four lakes was the result of the differences in the rate of increase in bicarbonate concentration in the various layers. During summer stagnation, bicarbonate gradually increased in the epilimnion with similar increases in calcium and salinity concentrations, particularly in Yudle North. In the hypolimnion, bicarbonate was released from the sediments, but the increase in alkalinity remained the greatest toward the bottom because the increase in concentration increased the density of water (Hutchinson 1957). In the metalimnion, diluted water low in bicarbonate was trapped at the beginning of thermal stratification, but later some bicarbonate originating from the sediments presumably was distributed by vertical turbulence (Hutchinson 1957). This increase, however, was less than that in the epilimnion and hypolimnion. The inverse clinograde distribution in total alkalinities under the ice was also caused by the release of bicarbonate from the sediments which was enhanced by the increase in salinity originating from road salting in Pine Hill and Yudle North Ponds.

TABLE 11. The mean, range of values, and number of observations of daily primary production per unit volume at optimum light (P-max) between May and October, 1969 and May and August, 1970 in the five lakes studied in Newfoundland. Days with P-max at the surface are excluded.

Pond	mg C/m³ max/day		N
	Mean	Range	
Bluehill North	11.9	4.1–24.3	10
Bluehill South	8.4	2.3–14.4	10
Pine Hill	22.6	5.8–51.0	18
Minchin	16.1	8.1–34.8	9
Yudle North	13.4	7.1–18.0	11

TABLE 12. The mean, range of values, and number of observations of daily primary production per unit surface area of the sampling station (P-area) between May and October, 1969 and May and August, 1970 in the five lakes studied in Newfoundland.

Pond	mg C/m²/day		N
	Mean	Range	
Bluehill North	25.6	10.8–51.5	13
Bluehill South	26.4	8.9–70.7	15
Pine Hill	58.6	9.5–152.7	25
Minchin	32.0	11.8–63.9	13
Yudle North	28.0	5.5–50.9	17

TOTAL PHOSPHORUS

Total phosphorus concentration, which is considered a nutrient of major importance in production (see Hutchinson 1957; Vollenweider 1968) was particularly low, but was comparable to the values (5–18 mg P/m³) reported by Rigler (1964) for Precambrian lakes in Algonquin Provincial Park, central Ontario. However, in other Precambrian lakes in northwestern Ontario the total phosphorus concentration exceeded that in these five lakes usually by a factor of 2 or 3 (Armstrong and Schindler 1971).

COLOR

Range of color in the five lakes is within the range of values described in lakes surrounded by peat deposits (Hutchinson 1957; Gorham 1957; Kalff 1968; Armstrong and Schindler 1971). Color gives a good indication of dissolved organic matter in water (Hutchinson 1957). High correlation exists between water color and levels of dissolved organic carbon in lakes in Sweden (Forsberg 1967). His derived equation for the estimation of dissolved organic carbon from color suggests a range of dissolved organic carbon values from 6–12 mg/liter in the five lakes.

Seasonal and annual variation in color in surface waters was the reverse of that described for salinity. In lakes which have no other large lakes in their catchment areas, color is mainly a function of influent water. During appreciable runoff color was usually highest, and increased after heavy rain. Consequently, in August and early September, 1969, when the water input was lowest, water color was low when, with the exception of Minchin, color did not exceed 20 Hazen units in surface waters. Minchin, which had the highest average color and little seasonal variation, maintained a relatively high color during the summer (Fig. 15). This is because the large volume of Big Pond on its catchment area acts as a buffer against appreciable seasonal variation in color.

Schindler (1971b) suggested that in an area, if the vegetation and soils are uniform, color of lakes should be proportional to the area of terrestrial drainage per lake surface (A"/A) and in the absence of inflow the humic color of lake water changes very little. Figure 16 suggests that terrestrial vegetation and soils are not uniform on the drainages and that other lakes in the catchment areas modify the relation between A"/A and color in the five lakes. The A"/A ratios are almost identical in Pine Hill and Yudle North, yet the latter which receives more bog drainage is more colored. Also, Bluehill North and Minchin are less colored than the proportionality to A"/A would suggest. Each of these lakes has a large lake on its catchment area, which represents 25 and 15% of the catchment areas, respectively. Not only the areas taken up by water bodies are lost as a potential source of colored humic substances, but excess rainwater that falls directly on these lake surfaces dilutes color originating from terrestrial drainage. Thus, large water bodies in the catchment areas tend to have water color reduced by dilution and when the volumes of these water bodies are large, the extent of temporal and annual variation is reduced also.

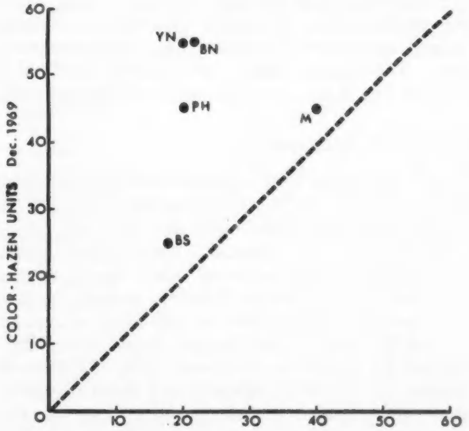


FIG. 15. A comparison of water color measurements (unfiltered samples) in Bluehill North (BN), Bluehill South (BS), Minchin (M), Pine Hill (PH), and Yudle North (YN) ponds, done in August and December, 1970. The broken diagonal line is the locus of equal values.

TEMPERATURE

The five lakes all have pronounced thermal stratification but with hypolimnia well above 4 C. Thus, they fit the description of the second-order lakes (Whipple 1898, cited in Hutchinson 1957). Pine Hill sometimes has only one circulation period in 1 yr, in the autumn. The combination of

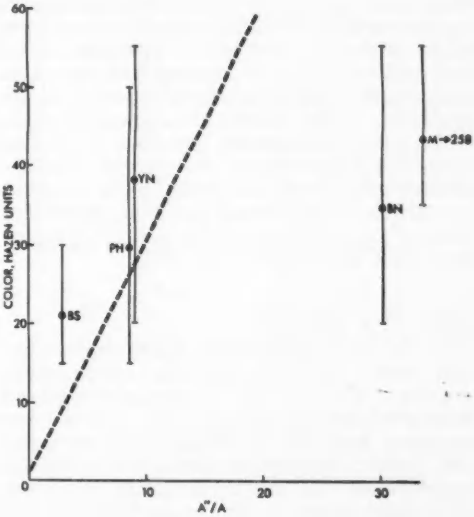


FIG. 16. The relationship between average water color, based on mean monthly values taken during the ice free period in 1969 and the relative basin size (A"/A) in Bluehill North (BN), Bluehill South (BS), Minchin (M), Pine Hill (PH), and Yudle North (YN) ponds in Newfoundland. Average water color values are indicated by solid, black circles, and the range of values by vertical lines. The diagonal broken line is the trend in 14 lakes in northwestern Ontario (Schindler 1971b).

small surface area, protection from the wind, and the relatively high level of dissolved solids in the deep part of the lake apparently prevents full vernal circulation, such as it was observed in 1970. The other four lakes are classically dimictic. The distribution of moderate epilimnetic and relatively high hypolimnetic temperatures are controlled by the windy, cool, oceanic climate of the area. Because of the gently sloping basins, thermal stratification develops only in a small percentage of the total water volume in Pine Hill and Bluehill North, which in turn is reflected in the increased heat budget of these lakes.

The large differences in the heat budgets of the six lakes considered in Table 4 are the result of similar differences in their mean depths, in accordance with that stated by Gorham (1964). It is also clear from these data that lakes without hypolimnia take up more heat for a given mean depth in the summer, 33% more on average than lakes with hypolimnia. The lakes studied in a continental climate would have much greater average differences between their epilimnetic and hypolimnetic temperatures. To facilitate the comparison of the summer heat income of the lakes studied with those situated in a continental climate in northwestern Ontario, one degree of latitude north of the study area, the data of Schindler (1971a) was used expressing the summer heat income as heat absorbed per meter depth according to the procedure of Fish (1970). This expression made direct comparison possible for lakes of various mean depths. As expected, the extreme values for summer heat incomes, 960 cal/cm^2 per m for stratified lakes and 2100 cal/cm^2 per m for unstratified lakes, in the continental climate were much greater than those determined in this study.

DISSOLVED OXYGEN

The lack of supersaturation of dissolved oxygen with respect to air-saturation in surface waters was obviously the result of low photosynthetic activity encountered in this study, and the low percentage values were caused by bacteria associated with humic substances, as indicated by relatively intense water color (Yoshimura 1938; Hutchinson 1957; Smith 1961).

OXYGEN DEFICIT

The three lakes in which relative hypolimnetic oxygen deficits were calculated have water color values of 20 Hazen units or more. Hutchinson (1938) suggested that oxygen deficits are misleading if the water color exceeds 10 Jackson units, because it is not possible to differentiate between the oxygen utilization in the hypolimnion by autochthonous and allochthonous organic matter (Strøm 1931). It is possible that a considerable part of the oxygen deficit, particularly in Yudle North and more so in Minchin, was caused by allochthonous humic substances and not from organic matter produced within the lake. The upper limit of the hypolimnion, 13 m, in Bluehill South is below the photic zone; thus, a low estimate of deficit due to photosynthesis was not introduced (Riley 1939). The upper hypolimnion at 5.5 and 6.5 m in Minchin and Yudle North respectively were approximately at compensation depths, thus errors due to photosynthetic oxygen supply to the hypolimnion were minimal. In addition to the presence of humic substances, the relatively high temperatures in the hypolimnia, particularly in Bluehill South, undoubtedly caused positive errors in the rates of oxygen deficits obtained. Even without considering the contribution of these two sources of possible errors to the oxygen deficits, the three lakes could be regarded as oligotrophic by applying the criteria set by Hutchinson (1957). In fact, the observed oxygen deficit in Bluehill South, which has the least colored water, would suggest a high degree of oligotrophy. If allowance were given for the decomposition of allochthonous organic matter and the hypolimnetic oxygen uptake due only to autochthonous organic production, the oxygen deficits obtained for the three lakes should be considerably reduced. By making these assumptions, the three lakes could be considered as extremely oligotrophic, characterized by low levels of endogenous organic production. The measurements of primary production obtained in these lakes support these assumptions.

PRIMARY PRODUCTION

It is probable that aquatic macrophytes make only a minor contribution to primary production in the three shallowest lakes and they are unimportant in the two deepest lakes. Chemo-organic production would probably play an important role in four lakes where dissolved organic matter, as measured by water color, is high either seasonally or year round. It would be least important in Bluehill South, which has the lowest level of dissolved organic matter. It is certain that a closer examination of periphyton, chemo-organic, and aquatic macrophyte production would be necessary before a complete estimate of primary production would be obtained in the five lakes. Problems arising in measuring primary production in these shallow lakes is the subject of a separate paper (Kerekes 1974a).

The primary production per unit volume at optimum light (P-max) is particularly valuable for the biological characterization of different waters regarding their primary trophic state (Rodhe 1958). Based on the P-max values, Pine Hill has the most productive water in this study because both the mean and the maximum P-max values were the highest among the five lakes, while Bluehill South, which had the lowest rate of water renewal, had the least productive water.

The five lakes are rated oligotrophic, based on their primary production rates unit surface area (P-area), according to the scheme of classification proposed by Rodhe (1969).

The highest midsummer P-max values in the five lakes were comparable to those in lakes described as primarily oligotrophic by Rodhe (1958), Dickman (1969), Johnson et al. (1970), and Schindler and Holmgren (1971) from different geographical regions (Table 13). Vinberg (1963) stated that in primary oligotrophic lakes, the rate of photosynthesis of plankton, at the surface in midsummer, is usually not more than 0.1 mg O_2/liter per day or about 37 mg C/m^3 per day gross production. According to his results, roughly 50% or more of this would be required for respiration, thus his figure for gross production would represent approximately not more than 18 mg C/m^3 per day net production at the surface. The five lakes certainly fit into this category of primary oligotrophic lakes. Considerably lower midsummer P-max values in the range of 0.2–0.7 mg C/m^3 max/day were reported by Olson and Odlaug (1966), Larson (1970), and Schindler and Holmgren (1971) for deep, exceptionally oligotrophic lakes (Table 13) and by Johnson et al. (1970) from a primarily oligotrophic lake contaminated with acid wastes on the Canadian Shield in Ontario.

Schindler and Holmgren (1971) described lakes on the Canadian Shield with midsummer P-max values in the range of 80–160 mg C/m^3 per day. These authors used a correction factor of 1.2–6.1

TABLE 13. Hourly and daily rates of primary production measured with ^{14}C technique in some lakes of different geographical areas in midsummer.

Lake	mg Carbon				Reference
	m^3 max/h	m^3 max/day	m^2/h	m^2/day	
Bluehill North	2.0	16	4.7	38	This study
Bluehill South	1.7	13	6.3	50	This study
Minchin	4.1	30	7.3	64	This study
Pine Hill	4.5	46	13.6	138	This study
Yudle North	2.2	17	6.7	51	This study
Dunlop (Ont.)	2.5	–	12.6	130	Johnson et al. (1970)
Nanek (Alaska)	–	13.5	–	167	Goldman (1960)
Torne Trask (Lappland)	–	7.7[a]	–	93[a]	Rodhe (1958a)
Ransaren (Lappland)	–	11.4[a]	–	66[a]	"
Marion (B.C.)	3.0	–	–	–	Dickman (1969)
Superior (Ont.)	0.7	–	–	183	Olson and Odlaug (1966)
Crater (Oreg.)	0.4	–	21.4	225	Larson (1970)
Weldo (Oreg.)	0.4	–	5.1	50	"
Odell (Oreg.)	30.0	–	223.0	2230	"
305 (Ont.)	–	142.0	–	850	Schindler and Holmgren (1971)
239 (Ont.)	–	22.0	–	550	" "
E. Winnipeg (Man.)	–	30.0	–	50	" "
Great Slave (N.W.T.)	–	2.0	–	100	" "
Esrom (Denmark)	–	935.0	–	1510	Jonasson and Kristiansen (1967)
Babine (B.C.)	–	–	10.2	–	Narver (1967)
Valkiajarvi (Finland)	–	30	–	146	Merliäinen (1970)
Tahoe (Calif.)	0.2	–	70.0	–	Goldman (1968a)
Cedar (Calif.)	2.3	–	6.0	–	"

[a] Upward correction by 45% (Goldman 1968b) not included.

times for a filtration error. When the maximum value for this correction is applied, the P-max values obtained in this study would be comparable to that reported by Schindler and Holmgren (1971). If, however, a mean correction factor was employed, the P-max values in the five lakes would have been in the lower range or somewhat below the values given by these authors. The latter assumption seems more reasonable when the hypolimnetic oxygen conditions in lakes with similar transparencies and presumably with similar amounts of dissolved allochthonous organic matter are compared from the two regions. Lake 305 (Brunskill and Schindler 1971; Schindler 1971a) is similar to Bluehill South except that it is somewhat deeper (z_m = 32.7 m and $\bar{z}$ = 15.1 m, respectively) and has somewhat higher transparency (7.5 m Secchi disc), showed considerably lower oxygen levels at the end of August (45% air-saturation) and at the end of February (30% air-saturation) at 29 m. The higher oxygen uptake in the hypolimnion in Lake 305 in spite of its lower content of dissolved organic matter, estimated from transparency, and its greatre mean depth, suggest that Lake 305 has a higher rate of primary production than Bluehill South.

The higher concentrations of total phosphorus and its various components (inorganic, particulate, and total dissolved), and the higher rate of phosphorus supply in the northwestern Ontario lakes, including Lake 305 (Armstrong and Schindler 1971), would suggest also a higher rate of primary production in those lakes.

The highest midsummer daily P-area rates were very low for these five lakes compared to those of other oligotrophic lakes selected from different geographical areas. Mainly oligotrophic lakes with low P-max rates were chosen for inclusion in Table 13, but one highly eutrophic lake was also included for contrast. The low P-area rates in the five lakes were the result of the restricted euphotic zones in the colored waters. Cedar Lake in California (Goldman 1968a) and Dunlop Lake in Ontario (Johnson et al. 1970) had P-max rates comparable to those in Yudle North and Bluehill North. In Cedar Lake, which is shallow (z_m = 4 m) and has highly colored water, the P-area rate is comparable to that in Yudle North and Bluehill North, but in Dunlop Lake, which has a deep euphotic zone, the P-area rates are more than twice as great. The inadequacy of comparing lakes based on P-area alone is obvious from the figures in Table 13.

EFFECT OF DRAINAGE BASIN ON PRIMARY PRODUCTION.

Kerekes (1973a, b) suggested that nutrient supply and nutrient levels are controlled by the rate of water renewal, as are features which depend on nutrient levels.

The relation between the mean P-max and the highest P-max rates and water renewal coefficients (Fig. 17) suggests the same kind of relation that occurred with the total phosphorus concentrations in the five lakes (Kerekes 1973a). Total phosphorus concentration per unit volume representative of the whole lake has a curvilinear relation to the water renewal coefficient, with total phosphorus beginning to decline when water renewal exceeds an optimum rate. Once that inflection is passed, the increase in water renewal will increasingly reduce nutrient levels and primary production by the displacement of phytoplankton and seston, hence total phosphorus concentration, irrespective of the increase in nutrient supply. He also explained why Bluehill North, Pine Hill, and Minchin depart from the suggested curve. The close agreement of mean P-max and maximum P-max rates with total phosphorus concentrations, suggests that phosphorus is a major factor in limiting primary production in the five lakes. This is in agreement with the findings of Bringman and Kühn (1965) that where the overall production is low, phosphorus is usually the limiting factor.

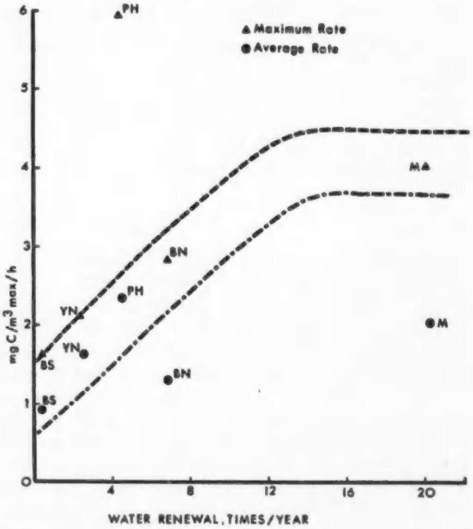


FIG. 17. The suggested relationship (indicated by broken line) between primary production of optimum light (P-max) measured between May and October, 1969 and May and August, 1970 and water renewal rate in Bluehill North (BN), Bluehill South (BS), Minchin (M), Pine Hill (PH), and Yudle North (YN) ponds in Newfoundland.

A similar curvilinear relation (not plotted) occurred between mean monthly chlorophyll *a* concentrations (Table 10) and water renewal rates in the five lakes.

LITTORAL EFFECT ON BASIN VOLUME

Rawson (1960) suggested that the values of shoreline development as an expression of the potential effect of littoral processes on the lake may be misleading when used to compare lakes which differ greatly in area. He proposed the ratio of shore length (L) to area (A) to compare lakes different in size. The L:A ratio has a shortcoming in that it relates the littoral effect to the surface area only, without considering its influence on basin volume. A more meaningful morphometric index could be obtained when the L:A ratio is divided by the mean depth ($\bar{z}$), where the littoral effect on basin volume is reflected. This method of computation when compared to the L:A ratio not only produced a greater numerical span between extreme values in the lakes, but it also reversed the relative positions of Bluehill North and Minchin. The modifying effect of (L:A)/$\bar{z}$ ratio on nutrient conditions and primary production in the five lakes could not be determined quantitatively, but all other factors being equal, a lake with a high (L:A)/$\bar{z}$ ratio would have richer inshore environment per unit volume and probably higher production. The low (L:A)/$\bar{z}$ ratio in Minchin Pond and the very high ratio in Pine Hill Pond were probably at least partially responsible for the similar departures of primary production from the curve suggested in Fig. 17.

Acknowledgments

I acknowledge my gratitude to Mr J. P. Cuerrier, Canadian Wildlife Service, who has provided help, ideas, and continuous encouragement during this study. I am much indebted to Mr P. Schwinghamer for providing excellent assistance in various phases of this project, and to Drs E. T. Garside and D. R. Flook for comments on the manuscript. Parks Canada provided working facilities and field assistance.

AMERICAN PUBLIC HEALTH ASSOCIATION, AMERICAN WATER WORKS ASSOCIATION, AND WATER POLLUTION CONTROL FEDERATION. 1965. Standard methods for the examination of water and wastewater. 12th ed. New York, N.Y. 769 p.

ANDERSON, R. S. 1971. Crustacean plankton of 146 alpine and subalpine lakes and ponds in western Canada. J. Fish. Res. Board Can. 28: 311–321.

ANON. 1970. Monthly meteorological summary. A record of observations taken at Gander, Nfld. Dep. Transp., Canada. Meteorol. Div. UDC-551-506.1 (718) (mimeo.)

ARMSTRONG, F. A., AND D. W. SCHINDLER. 1971. Preliminary chemical characterization of waters in the Experimental Lakes Area, northwestern Ontario. J. Fish. Res. Board Can. 28: 171–187.

ARTHUR, C. R., AND F. H. RIGLER. 1967. A possible source of error in the ^{14}C method of measuring primary productivity. Limnol. Oceanogr. 12: 121–124.

BRINGMANN, G., AND R. KÜHN. 1965. Nitrat oder Phosphat als Begrenzungfaktor des Algenwachstums. Gesundheits-Ing. Jg. 86: 210–214.

BRUNSKILL, G. J., AND D. W. SCHINDLER. 1971. Geography and bathymetry of selected lake basins, Experimental Lakes Area, northwestern Ontario. J. Fish. Res. Board Can. 28: 139–155.

DAVIS, C. C. 1972. Plankton dynamics in a Newfoundland lake. Verh. Int. Ver. Limnol. 18: 278–283.

DICKMAN, M. 1969. Some effects of lake renewal on phytoplankton productivity and species composition. Limnol. Oceanogr. 14: 660–666.

FISH, G. R. 1970. A limnological study of four lakes near Rotura. N. Z. J. Mar. Freshwater Res. 4: 165–194.

FORSBERG, G. 1967. Dissolved organic carbon in some lakes in Uppland, Sweden. Oikos 18: 210–216.

GOLDMAN, C. R. 1960. Primary productivity and limiting factors in three lakes of the Alaska Peninsula. Ecol. Monogr. 30: 207–230.

1968a. Aquatic primary production. Am. Zool. 8: 31–42.

1968b. The use of absolute activity for estimating serious errors in the measurement of primary productivity with C14. J. Cons. Int. Explor. Mer 32: 172–179.

GOLTERMAN, H. L., AND R. S. CLYMO [ed.] 1969. Methods for chemical analysis of fresh water. IBP Handbook No. 8, Blackwell Scientific Publ., Oxford. 172 p.

GORHAM, E. 1957. The chemical composition of lake waters in Halifax County, Nova Scotia. Limnol. Oceanogr. 2: 12–21.

1964. Morphometric control of annual heat budgets in temperate lakes. Limnol. Oceanogr. 9: 525–529.

HARE, F. K. 1952. The climate of the island of Newfoundland. A geographical analysis. Canada Dep. Mines Tech. Surv. Geogr. Bull. 2: 36–38.

HUTCHINSON, G. E. 1938. On the relations between the oxygen deficit and the productivity and typology of lakes. Int. Rev. Hydrobiol. 36: 336–355.

1957. A treatise on limnology. Vol. I. John Wiley and Sons, Inc., New York, N.Y. 1015 p.

JENNESS, S. E. 1963. Terra Nova and Bonavista map-areas, Newfoundland. (2 DE ½ and 2 C). Dep. Mines Tech. Surv. Geol. Surv. Can. Mem. 327: 184 p.

JOHNSON, M. G., M. F. P. MICHALSKI, AND A. E. CHRISTIE. 1970. Effects of acid mine wastes on phytoplankton communities of two northern Ontario lakes. J. Fish. Res. Board Can. 27: 425–444.

Jonasson, P. M., and J. Kristiansen. 1967. Primary and secondary production in Lake Esrom. Growth of *Chironomus anthracinus* in relation to seasonal cycles of phytoplankton and dissolved oxygen. Int. Rev. Gesamten Hydrobiol. 52: 163–217.

Kalff, J. 1967. Phytoplankton dynamics in an arctic lake. J. Fish. Res. Board Can. 24: 1861–1871.

1968. Some physical and chemical characteristics of arctic fresh waters in Alaska and northwestern Canada. J. Fish. Res. Board Can. 25: 2575–2587.

Kerekes, J. 1968a. A brief survey of twenty-one lakes in Terra Nova National Park, Newfoundland. Can. Wildl. Serv. MS Rep. 60 p.

1968b. The chemical composition of lake waters in Terra Nova National Park, Newfoundland. Can. Wildl. Serv. MS Rep. 18 p.

1972. A comparative limnological study of five lakes in Terra Nova National Park, Newfoundland. Ph.D. Thesis. Dalhousie Univ., Halifax, N.S. 388 p.

1973a. The influence of water renewal on the nutrient supply in small, oligotrophic (Newfoundland) and highly eutrophic (Alberta) lakes, p. 383–400. *In* Proc. Lakes of Western Canada Symp., Univ. Alberta, Edmonton, Alta.

1973b. Limological conditions in thirty lakes. Aquatic Resource Inventory, Part 5. Kejimkujik National Park, N.S. Can. Wildl. Serv. MS Rep. 53 p.

1974a. The influence of basin morphometry on the primary production in five small oligotrophic lakes in Newfoundland. Proc. Symp. on Limnology of Shallow Waters, Tihany, Hungary. (In press)

1974b. Factors influencing planktonic primary production in five small oligotrophic lakes in Newfoundland. (In preparation)

Kerekes, J., and P. Schwinghamer. 1973. Aquatic resource inventory, Gros Morne National Park. Can. Wildl. Serv. MS Rep. 35 p.

Larson, D. W. 1970. On reconciling lake classification of four oligotrophic lakes in Oregon. Ph.D. Thesis. Oregon State Univ., Corvallis, Oreg. 145 p.

Menzel, D. W., and N. Corwin. 1965. The measurement of total phosphorus in sea water based on the liberation of organically bound fractions by persulfate oxidation. Limnol. Oceanogr. 10: 280–282.

Meriläinen, J. 1970. On the limnology of the meromictic Lake Valkigjarvi, in the Finnish Lake District. Ann. Bot. Fenn. 7: 29–51.

Narver, D. W. 1967. Primary productivity in the Babine Lake System, British Columbia. J. Fish. Res. Board Can. 24: 2045–2052.

Olson, T. A., and T. O. Odlaug. 1966. Limnological observations on the western Lake Superior. Great Lakes Res. Div., Univ. Michigan, Publ. 15: 109–118.

Rawson, D. S. 1960. A limnological comparison of twelve large lakes in northern Saskatchewan. Limnol. Oceanogr. 5: 195–211.

Reeves, C. C. 1968. Introduction to paleolimnology. Elsevier Publishing Co., New York, N.Y. 228 p.

Reid, G. K. 1961. Ecology of inland waters and estuaries. Reinhold Publishing Corp., New York, N.Y. 375 p.

Rigler, F. H. 1964. The phosphorus fractions and the turnover time of inorganic phosphorus in different types of lakes. Limnol. Oceanogr. 9: 511–518.

Riley, G. A. 1939. Limnological studies in Connecticut, Part I. General limnological survey. Ecol. Monogr. 9: 53–66.

Rodhe, W. 1949. The ionic composition of lake waters. Verh. Int. Ver. Limnol. 10: 377–386.

1958. The primary production in lakes: some results and restrictions of the C14 methods. Rapp. P.-V. Réun. Cons. Perm. Int. Explor. Mer 144: 122–128.

1964. Effects of impoundment on water chemistry and plankton in Lake Ransaren (Swedish Lappland). Verh. Int. Ver. Limnol. 15: 437–443.

1969. Crystallization of eutrophication concepts in northern Europe, p. 50–64. *In* Proc. of the International Symp. on Eutrophication, Madison, Wisconsin, 1967.

Ruttner, F. 1953. Fundamentals of limnology. Univ. Toronto Press, Toronto, Ont. 242 p.

Saunders, G. W., F. B. Trama, and R. W. Bachmann. 1962. Evaluation of a modified C-14 technique for shipboard estimation of photosynthesis in large lakes. Univ. Mich. Great Lakes Res. Div. Publ. No. 8: 1–61.

Schindler, D. W. 1971a. Light, temperature, and oxygen regimes of selected lakes in the Experimental Lakes Area, northwestern Ontario. J. Fish. Res. Board Can. 28: 157–169.

1971b. A hypothesis to explain differences and similarities among lakes in the Experimental Lakes Area, northwestern Ontario. J. Fish. Res. Board Can. 28: 295–301.

Schindler, D. W., and S. K. Holmgren. 1971. Primary production and phytoplankton in the Experimental Lakes Area, northwestern Ontario, and other low-carbonate waters, and a liquid scintillation method for determining ^{14}C activity in photosynthesis. J. Fish. Res. Board Can. 28: 189–201.

Smith, M. W. 1961. A limnological reconnaissance of a Nova Scotian brown water lake. J. Fish. Res. Board Can. 18: 463–478.

1963. The Atlantic Provinces in Canada, p. 521–534. *In* D. G. Frey [ed.] Limnology of North America. Univ. Wisconsin Press, Madison, Wis.

Steemann Nielsen, E. 1952. The use of radioactive carbon (C-14) for measuring organic production in the sea. J. Cons. Int. Explor. Mer 18: 117–140.

1958. Experimental methods for measuring organic production in the sea. Rapp. P.-V. Réun. Cons. Perm. Int. Explor. Mer 144: 38–46.

Strickland, J. D. H., and T. R. Parsons. 1968. A practical handbook of seawater analysis. Bull. Fish. Res. Board Can. 167: 311 p.

STRØM, K. M. 1931. Feforvatn. A physiographic and biological study of a mountain lake. Arch. Hydrobiol. 22: 491–536.

THOMAS, J. F. J. 1953. Scope, procedure, interpretation of survey studies. Water Surv. Rep. 1, Queen's Printer, Ottawa. 60 p.

VINBERG, G. G. 1963. The primary production of bodies of water. U.S. A. E. C. Div. Tech. Serv. Transl. AEC-tr-5692: 601 p.

VOLLENWEIDER, R. A. 1968. The scientific basis of lake and stream eutrophication, with particular reference to phosphorus and nitrogen as eutrophication factors. Organ. Econ. Coop. Dev. (Paris) DAS/CSI/68 Tech. Rep. 27: 1–182.

[ed.] 1969. A manual on methods for measuring primary production in aquatic environments. (Including chapter on bacteria.) IBP Handbook No. 12. Blackwell Scientific Publ., Oxford. 213 p.

VOLLENWEIDER, R. A., AND A. NAUWERCK. 1961. Some observations on the C-14 method for measuring primary production. Verh. Int. Ver. Limnol. 14: 134–139.

WATT, W. D. 1965. A convenient apparatus for in situ primary production studies. Limnol. Oceanogr. 10: 298–300.

WELCH, P. S. 1948. Limnological methods. McGraw-Hill Book Co. Inc., Toronto, Ont. 381 p.

WHIPPLE, G. C. 1898. Classifications of lake according to temperature. Am. Nat. 32: 25–33.

YENTSCH, C. S., AND D. W. MENZEL. 1963. A method for the determination of phytoplankton chlorophyll and phaeophytin by fluorescence. Deep-Sea Res. 10: 221–231.

YOSHIMURA, S. 1938. Dissolved oxygen of the lake waters of Japan. Tokyo Bunrika Daigaku Sect. C. Sci. Rep. 8: 63–277.

Physical and Chemical Limnology of Char Lake, Cornwallis Island (75° N Lat.)[1]

D. W. SCHINDLER, H. E. WELCH,[2] J. KALFF,[3] G. J. BRUNSKILL, AND N. KRITSCH
Department of the Environment, Fisheries and Marine Service
Freshwater Institute, Winnipeg, Man. R3T 2N6

SCHINDLER, D. W., H. E. WELCH, J. KALFF, G. J. BRUNSKILL, AND N. KRITSCH. 1974. Physical and chemical limnology of Char Lake, Cornwallis Island (75° N lat.). J. Fish. Res. Board Can. 31: 585–607.

Seasonal data for several physical and chemical variables in Char Lake are given. Annual cycles of major solutes are influenced primarily by freeze–thaw cycles. Concentrations of most substances are increased by freezing-out during the winter. Because the lake does not circulate during maximum spring meltwater flow, this freezing-out maintains concentrations in the lake above those in inflow streams.

Concentrations of phosphorus and nitrogen in the lake are low throughout the year. Precipitation contains little phosphorus or nitrogen. Input of phosphorus and nitrogen are calculated to be 0.016 and 0.314 g/m², respectively. Retention of nutrients by the lake is lower than in temperate regions, although still quite efficient.

With the exception of silica, return of ions from the sediments during winter was found to be negligible.

Disturbance of one inflow stream due to airstrip construction caused great increases in concentrations of nitrogen, silica, chloride, sulfate, and bicarbonate in the stream.

SCHINDLER, D. W., H. E. WELCH, J. KALFF, G. J. BRUNSKILL, AND N. KRITSCH. 1974. Physical and chemical limnology of Char Lake, Cornwallis Island (75° N lat.). J. Fish. Res. Board Can. 31: 585–607.

Nous présentons des données relatives à plusieurs variables physiques et chimiques du lac Char. Le cycle annuel des substances dissoutes est avant tout affecté par les cycles de gel et de dégel. La teneur de la plupart des substances dissoutes augmente à la suite du gel en hiver. Puisque le lac ne circule pas pendant le débit maximal de la fonte des neiges au printemps, ce gel maintient les concentrations du lac à un niveau plus élevé que celui des cours d'eau d'entrée.

Les teneurs en phosphore et en azote dans le lac sont faibles pendant toute l'année. La précipitation renferme peu de phosphore ou d'azote. On calcule que l'entrée du phosphore et de l'azote s'élève à 0.016 et 0.314 g/m² respectivement. La rétention des substances nutritives par le lac est plus basse que dans les régions tempérées, quoique encore assez efficace.

A l'exception de la silice, le retour des ions des sédiments en hiver est négligeable.

Le dérangement d'un cours d'eau d'entrée lors de la construction d'une piste d'atterrissage a causé de fortes augmentations de teneurs en azote, silice, chlorure, sulfate et bicarbonate dans ce cours d'eau.

Accepted December 31, 1973

ALTHOUGH limnological research has been carried out in the arctic for several decades, data on high arctic lakes are still few (reviewed by Hobbie 1973). No published work describes complete annual cycles of physical and chemical events in a high arctic lake. The purpose of this paper is to describe such annual cycles in Char Lake, a small, (area = 52.6 ha; mean depth = 10.2 m; maximum depth = 27.5 m) clear lake near the village of Resolute, Cornwallis Island (74°42′N; 94°50′W). The lake was the site of a Canadian IBP study of freshwater productivity and its basic limnological features were described by Rigler (1972).

Description of the Lake Basin

The following is largely from Arkay (1972).

The land drainage to Char Lake is 435 ha in area. Bedrock in the area is typical Read Bay formation fossiliferous and dolomitic limestone of

---

[1] This paper, part of a special issue that comprises a comprehensive review of Limnology in Canada, was prepared to mark the 19th Congress of the International Association of Limnology (SIL), in Winnipeg, Man., during August 1974.

[2] Present address: (H. E. W.) Department of the Environment, Fisheries and Marine Service, Biological Station, St. Andrews, N.B.

[3] Present address: Department of Biology, McGill University, Montreal, Que.

Printed in Canada (J3259)

the Read Bay formation. The watershed of the lake is mantled with unconsolidated material, particularly frost-shattered limestone rubble. Some fluvial deposition is noticeable at the foot of major stream courses.

The basin is dominated by a steep northwest–southeast scarp on the northeast side of the lake. At the top of the scarp (120–150 m above sea level), a plateau forms the source of all three major inlet streams flowing to the lake (Fig. 1). The face of the scarp has a few areas of exposed bedrock, and a talus slope that extends into Char Lake on the steep northeastern shore. Other parts of the drainage basin are low, and gently rolling. Felsenmeer, nivation hollows, and patterned ground are common.

The area was glaciated at least once. The lake surface is 34 m above the sea, and probably emerged above the sea surface over 6000 yr ago (Barr 1971, Andrews et al. 1971). Permafrost underlies the entire area, with an active layer less than 0.5 m deep. Plant cover in the drainage basin is only 5–7%. *Saxifraga oppositifolia*, *S. caespitosa*, *Salix arctica*, and *Cerastium alpinum* are the commonest species of angiosperms.

Annual precipitation in the area averages 136 mm (McCann et al. 1972). Approximately half of this falls as rain between June and September. The rest accumulates as a drifted snow pack which melts in June and early July. Maximum snowfall occurs in September and October, with a secondary maximum in May (Hagglund 1958).

Estimates of evaporation and evapotranspiration in the high arctic are almost totally lacking, due chiefly to problems with standard evaporation pans, which freeze over at night and take a good part of the subsequent day to thaw. Hobbie (1973) quotes two sources indicating that only 15% of the precipitation is evaporated in arctic areas receiving 300–350 mm of precipitation. As Char Lake is at a higher latitude, it appears reasonable to assume that evaporation will not exceed this figure. Annual runoff from terrestrial drainage to the lake, therefore, should average between 374,000 m^3 (assuming 50 mm/year as evaporation) and 592,000 m^3 (assuming no evaporation). This would mean that the water renewal time for the lake is 9–14 yr.

Four small streams, which tend to dry up in late August, drain into Char Lake (Fig. 1). Streams #3 and #4 drain undisturbed ground. Stream #2 drains largely undisturbed ground but also receives some water from stream #1. Stream #1, the smallest, drains about 29 ha, much of which had the topsoil and gravel removed by the Ministry of Transport during 1969–72 for use as fill, and permafrost is continually being exposed and melted as thawed gravel is removed.

Methods

PHYSICAL

Lake temperatures were measured at 1-m intervals to the nearest 0.01 C with a calibrated thermistor thermometer. Ice thickness was measured near the center of the lake with a long pole marked in tenths of meters. Regression lines were fitted to the ice-thickness data from the freeze periods and comparison was made between years, by analysis of covariance. Polynomials were fitted to the data from complete freeze–thaw cycles. Snow measurements were made at irregular intervals at each of the 11 grid intersects (Fig. 1).

Surface irradiance was measured at lake-side with a Belfort pyrheliometer until September 1969, and thereafter with a model 67 Yellowsprings pyranometer and strip chart recorder located approximately 2 km from the lake. Fifty percent of the measured solar radiation was considered to fall in the visible portion of the spectrum. Subsurface irradiance was measured at approximately weekly intervals between May and September and biweekly at other times, using a GM submarine photometer with a Weston selenium photocell. Blue, green, and red glass filters having spectral ranges of 300–500, 460–660, and 500–720 nm, respectively, (Larson 1972) were used occasionally. During ice cover, a variable "hole effect"[4] was frequently noted to 5 m and occasionally to 10 m below the ice surface. Light readings from greater depths were therefore plotted on semilog paper and fitted by a straight line, which was extrapolated to the ice to give light energy entering the water. The average vertical extinction coefficients (*k*) were calculated on each date.

CHEMICAL

Measurements for oxygen, conductivity, pH, and alkalinity were made from 1969–72, and other chemical variables were monitored for a 1-yr period beginning May 1971. The lake was sampled every 2nd wk with a plexiglass van Dorn bottle (at depths of 0 m or the ice bottom, 1, 2, 3, 5, 7.5, 10, 15, 20, and 25 m) for conductivity, pH, and alkalinity; at 2-m intervals for oxygen, and at 5-m intervals for other chemical measurements. Samples were kept at lake temperature while being taken to the laboratory, where oxygen samples were fixed, alkalinity and pH determined immediately, and water for other chemical determinations was filtered through ignited (500 C, 1 h) Whatman GF/C glass-fiber filters.

Rain samples were taken from collectors constructed of plexiglass or polyethylene sheeting. All major rainfalls in 1971 were sampled and analyzed. Snowpack samples were collected and analyzed in late May and early

---

[4] A hole in the ice allows the entry of solar radiation which is normally excluded by ice and snow. A subsurface light meter held directly beneath the hole will therefore give high readings which are unrepresentative of true subsurface light conditions. This "hole effect" disappears deeper in the water column.

June, just before runoff commenced. Inflow and outflow streams were sampled at the edge of the lake, once or twice weekly during maximum runoff in June and early July, and less frequently through the rest of the summer.

Filtered, acid-preserved samples were air-shipped to the Freshwater Institute, Winnipeg, where Ca^{+2}, Mg^{+2}, Na^{+}, and K^{+} were analyzed by atomic absorption.

The material filtered from samples onto GF/C filters was dried in a desiccator; filters were shipped to Winnipeg for determination of carbon and nitrogen with a Perkin-Elmer model 240 Elemental Analyzer, and phosphorus by a spectrophotometric molybdenum blue method, after ignition at low temperature and acid extraction.

Samples for dissolved organic carbon analysis were filtered, acidified and bubbled, sealed in ampoules, and analyzed in Winnipeg by the gas-chromatographic method of Stainton (1973).

Sulphate and chloride were measured in Winnipeg by the ion-exchange method of Mackereth (1955).

The following analyses were done at the Resolute Bay laboratory: oxygen according to Carpenter (1965); ammonium nitrogen by the phenolhypochlorite method of Solorzano (1969); nitrate by reduction to nitrite (Wood et al. 1967) followed by analyses for nitrite (Bendschneider and Robinson 1952); soluble reactive phosphorus (Murphy and Riley 1962); total dissolved phosphorus and nitrogen after ultraviolet photochemical oxidation (Armstrong and Tibbitts 1968) followed by the above-mentioned phosphate and nitrate methods; total dissolved iron after ultraviolet photochemical oxidation followed by treatment with 1:10 phenanthroline (Armstrong 1957); and soluble reactive silica (Armstrong and Butler 1962). Conductivity was measured on a Beckman conductivity bridge and reported as μmho/cm corrected to 25 C.

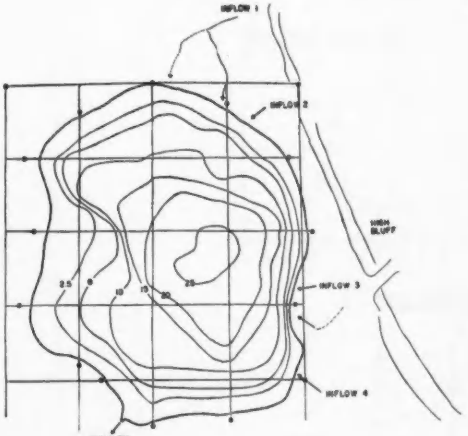


FIG. 1. A morphometric map of Char Lake, showing the sampling grid, the four major inflow streams, the outflow, and the location of the bluff. Depths are in meters. ⊙ shows the locations of markers used for locating positions on the lake.

Analyses for soluble reactive phosphorus, nitrate, and ammonia were done within a few hours of collection, and total dissolved phosphorus, nitrogen, iron and soluble reactive silica within 24 h.

The mass (M) of each element in the lake on any sampling date was calculated:

$$M = \int_{z = z_0}^{z = z_m} A_z \, C_z \, d_z$$

where A_z is the lake area and C_z the concentration of element at each sampling depth z, from the ice surface to the bottom of the lake. On winter dates when samples were not taken directly beneath the ice surface, the 5-m value for C_z was used at 0 m. This would cause slight underestimates on those dates, but should not affect the rough calculations done here.

Sediments were sampled with a modified mini-Mackereth corer (Mackereth 1969). These were extruded the same day, and interstitial waters were removed with a Reeburgh (1967) press, filtered through Whatman GF/C glass-fiber filters, and shipped to the Freshwater Institute, Winnipeg, for analysis. Details of analytical techniques are as given by Brunskill et al. (1971).

Results

PHYSICAL

In most years Char Lake is a typical cold, monomictic polar lake (never rising above 4 C, Forel 1892), with a brief summer overturn period of 0–6 wk (Fig. 2). The lake begins to cool in late August and freezes about September 18. When arctic lakes are cooling in the fall, winds are strong and constant (mean wind speed for September at Resolute is 11 km/h) and lakes cool well below 4 C before freezing. For example, in September 1969 Char Lake cooled to an average temperature of 0.2 C or less, under the influence of strong winds. The surface temperature was 0 C, ice crystals formed on the surface and accumulated on the windward shore, and fast ice built up on rocks in the littoral zone to a depth of 0.3 m before the lake sheeted over on a calm night. By contrast, in September 1971, calm conditions occurred while the lake was still relatively warm (Fig. 2b) and winter water temperatures were about 0.5 C warmer than in previous years.

Straight lines provide an adequate description of increase in ice thickness with time for the first part of the freeze period in Char Lake, and comparison of regression lines shows that the freezing rate is significantly different each year, probably reflecting both water temperature and snow cover. Maximum ice thickness occurred near May 25 each year (Fig. 3A).

Ice reached average maximum thickness of 2.2–2.4 m in the three winters when measurements were made. It occupied 1.0–1.1 × 10^6m^3, or 18–20% of the lake volume. At a density of 0.917 and latent heat of fusion of 79.7 cal/g, this represents 14,000 to 15,000 cal/cm^2. The difference between warmest summer water temperatures and coldest winter ones was an additional 2000–4000 cal/cm^2, so that the overall gross heat budget probably ranges from 16,000 to 19,000 cal/cm^2. As pointed out by Hutchinson (1957) these budgets are as high as for temperate or subarctic lakes, except that the latent heat of melting, rather than warming, is the most important term in the arctic heat budget.

The isotherms (Fig. 2) suggest a slight cooling of Char Lake over winter, and Meretta Lake (Schindler et al. 1974) clearly loses heat over winter. The warming period reported by Brewer (1958) beneath the ice of shallow lakes near Barrow in the fall does not occur in Char Lake, because of the low radiation levels in October and the rapid accumulation of snow after freeze-up.

A slight temperature inversion is present each July just below the ice surface (Fig. 2). Such inversions are common under ice during periods of high insolation, but usually disappear during the night in temperate regions (Hill 1967; D. W. Schindler, Department of the Environment, Freshwater Institute, Winnipeg, unpublished data). The high continuous input of solar radiation at Resolute in summer may help to maintain the inversion in spite of its instability. In late June, runoff from the watershed raises the water level in the lake. This, combined with thawing near the now snow-free shoreline, leads to formation of a moat which gradually widens until the ice is free-floating.

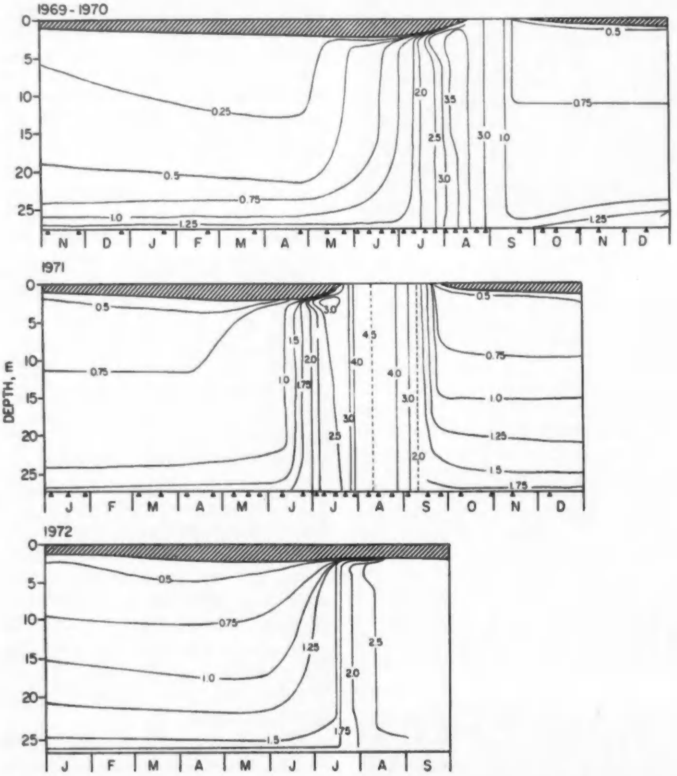


FIG. 2. Isotherms (C) for Char Lake, 1969–72. Shaded areas represent ice thickness.

In years with cold, cloudy summers this normal cycle is interrupted. For example, in 1972 the maximum summer water temperature was below normal and the lake remained ice-covered (Fig. 3B). Even though the maximum summer water temperature was below normal, the winter water temperature in 1972–73 was above normal, because the ice sheet prevented late summer mixing and cooling. The effects of residual ice are at least partly additive, as the average ice thickness on the central portion of Char Lake was about 2.9 m in May 1973.

Snow builds up rapidly in the fall, remains more or less constant over winter, then increases once more in spring (Fig. 4). If the early snowfall is sufficient to depress the ice surface below the

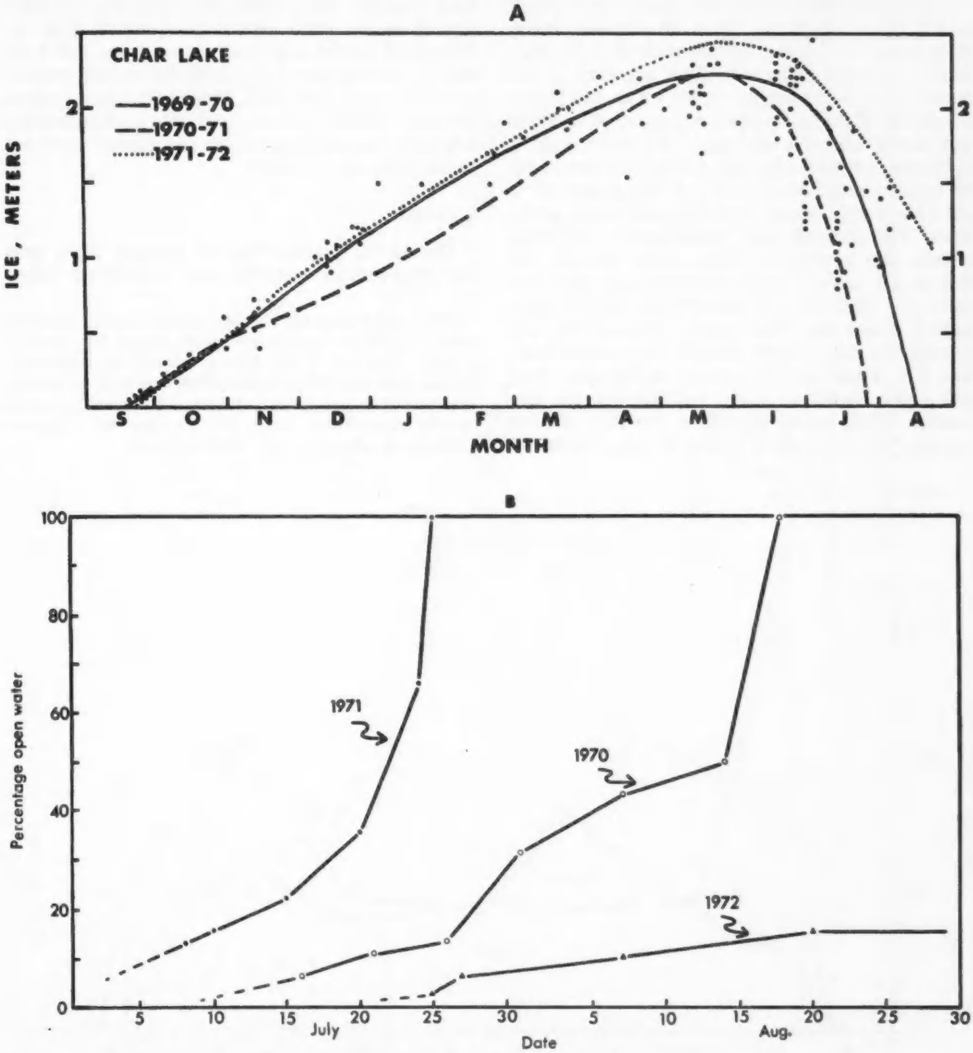


FIG. 3. A, The development of ice cover on Char Lake. B, The transition from ice cover to open water in Char Lake. The lake remained ice-covered in 1972.

water level, as in 1969, water will seep through cracks in the ice, wetting the snow and causing the formation of slush, or white ice (Shaw 1962). In 1969 wet snow lay on the ice into late November, despite ambient temperature down to -40 C, but the formation of extensive areas of slush ice on Cornwallis Island lakes is unusual because of the low snowfall. Severe storms in midwinter often erode more snow than they deposit (Fig. 4).

With the exception of the above-mentioned period in the fall of 1969, ice cover is normally highly transparent "black" ice virtually without air bubbles, which transmits light with high efficiency. Light reaching the lower surface of the ice is thus largely a function of the snow depth and seasonal variation in incident light. At the end of the polar night in February, a typical layer of 10–15 cm of snow (Fig. 4) allowed only about 1–2% of the irradiance to enter the water column until the onset of the spring thaw. For example, the disappearance of snow allowed the amount of light energy entering the lake to rise about tenfold between early June and early July 1970 (Fig. 5). During the typical ice-free period in late July and August, extensive fog and cloud-cover significantly reduced the incident light. The sun, which remains above the horizon from late April, dips below the horizon for the first time in mid-August, whereafter the days shorten rapidly. The polar night begins in early November and lasts until early February. Negligible light enters the lake during this period. In early spring the water was characterized by a low extinction coefficient (*k*), with maximum penetration in the green and blue portions of the spectrum (Table 1). The extinction coefficient increased slowly until the onset of the melt-off and moat formation. When ice left the lake in late July, turbidity increased still more, perhaps due to wind exposure.[5] Once the lake became ice-covered, the turbidity declined almost to the levels recorded in March (Fig. 6). Minimum Secchi disc readings of 5 m, 2.5–3 m, and 10 m were recorded during the ice-free seasons of 1970, 1971, and 1972. Pre-runoff Secchi values between 20 and 22 m are probably underestimates, reflecting the feeble subsurface irradiance under ice rather than the turbidity.

CHEMICAL

During the period of active freezing there were two conductivity maxima, one immediately below

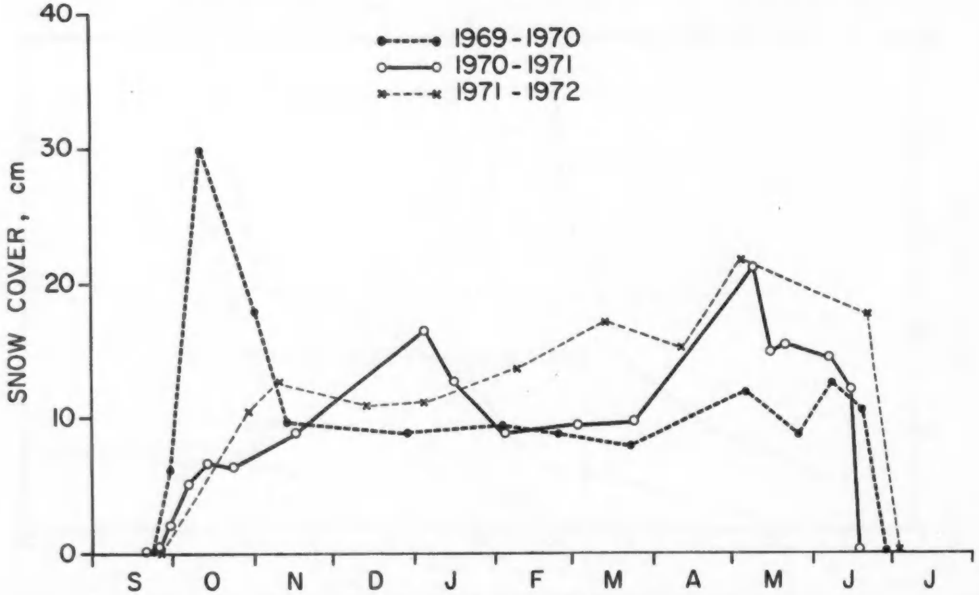


FIG. 4. Snow cover on Char Lake in the years of study.

---

[5] 1970 was somewhat atypical in this respect. In other years, turbidity decreased slightly during the ice-free period, although it was high compared to midwinter values. The high 1970 values were due to a rainstorm which occurred as ice left the lake. Apparently, runoff usually contributes more to the observed summer increase in turbidity than wind exposure.

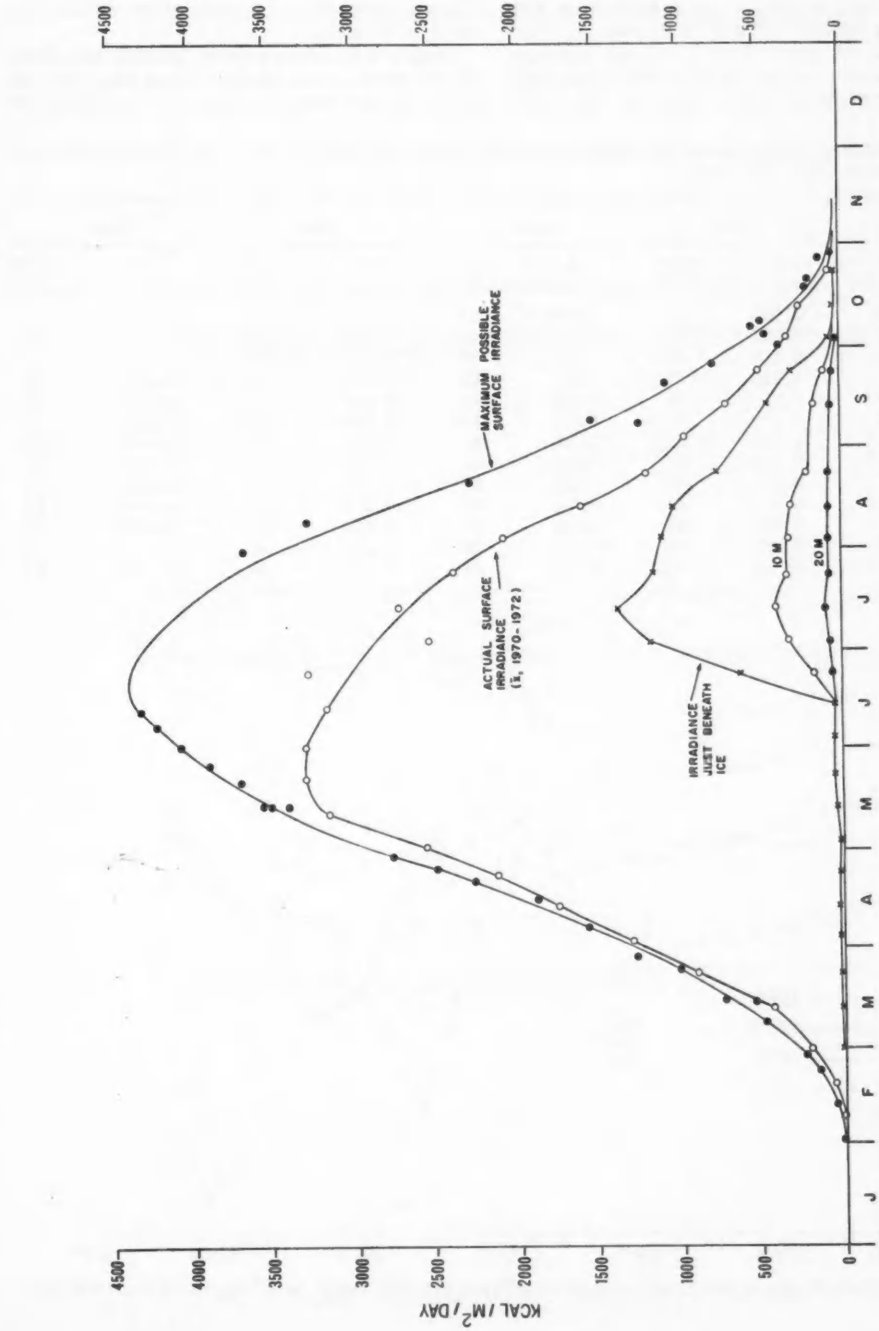


FIG. 5. Incident light at the lake surface and that penetrating ice, snow, and water to various depths in Char Lake. Figures are averages of 1971–72.

the ice and another, higher one at the bottom, with a minimum between 10 and 15 m (Fig. 7). When freezing ceased about June 1, mixing continued and conductivity became uniform with depth until the addition of meltwater began in late June. Average conductivity increased about 25% during the 3 yr of study.

Oxygen concentrations were greatest just under the ice when it was thickest in late May (Fig. 8), at which time values as low as 2.5 mg/liter were

TABLE 1. Average vertical extinction coefficients (*k*) and percent transmittance (% T) per meter for white and filtered light in Char Lake, 1970.

Date	White		Green		Blue		Red	
	k	% T	*k*	% T	*k*	% T	*k*	% T
Mar. 3, 1970	0.093	91	0.069	93	0.073	93	–	–
Apr. 5	0.125	88	0.109	90	0.090	91	–	–
Apr. 23	0.118	89	0.117	89	0.111	90	–	–
May 5	0.126	88	0.131	88	0.118	89	0.455	63
May 12	0.117	89	0.088	92	0.096	91	0.435	65
July 2	0.111	90	0.119	89	0.114	89	0.394	67
July 9	0.181	83	0.206	81	0.212	81	0.462	63
July 15	0.213	81	0.209	81	0.252	78	0.480	62
July 23	0.222	80	0.202	82	0.236	79	0.486	62
July 29	0.187	83	0.184	83	0.213	81	0.445	64
Aug. 6	0.163	85	0.141	87	0.158	85	0.430	65
Aug. 13	0.155	86	0.123	88	0.139	87	–	–
Aug. 23	0.109	90	0.127	88	0.128	88	0.461	63

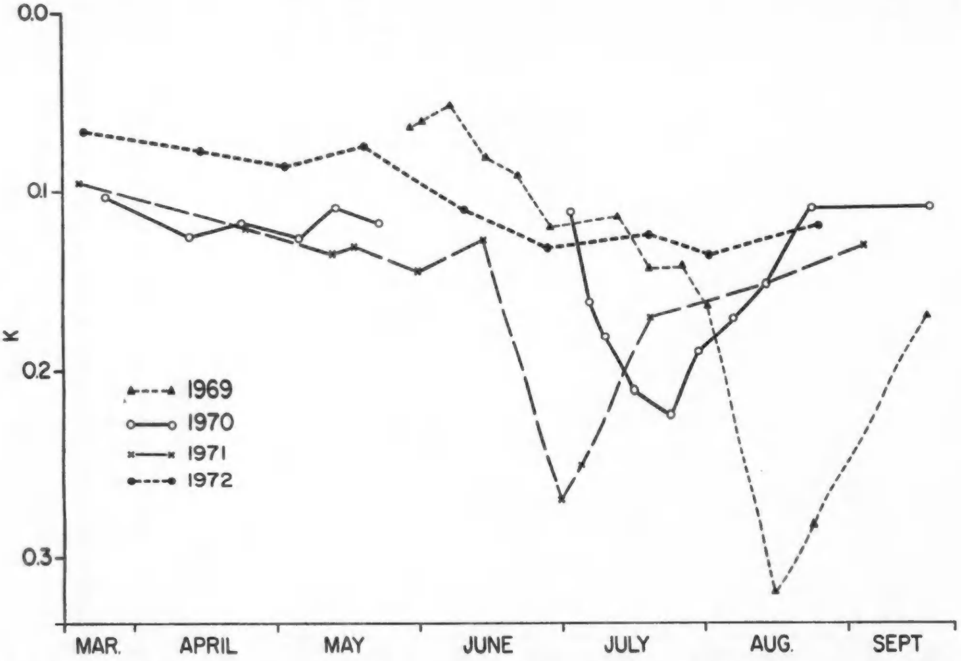


FIG. 6. Seasonal changes in the vertical extinction coefficient (*k*). Note higher turbidities during melt- and open water.

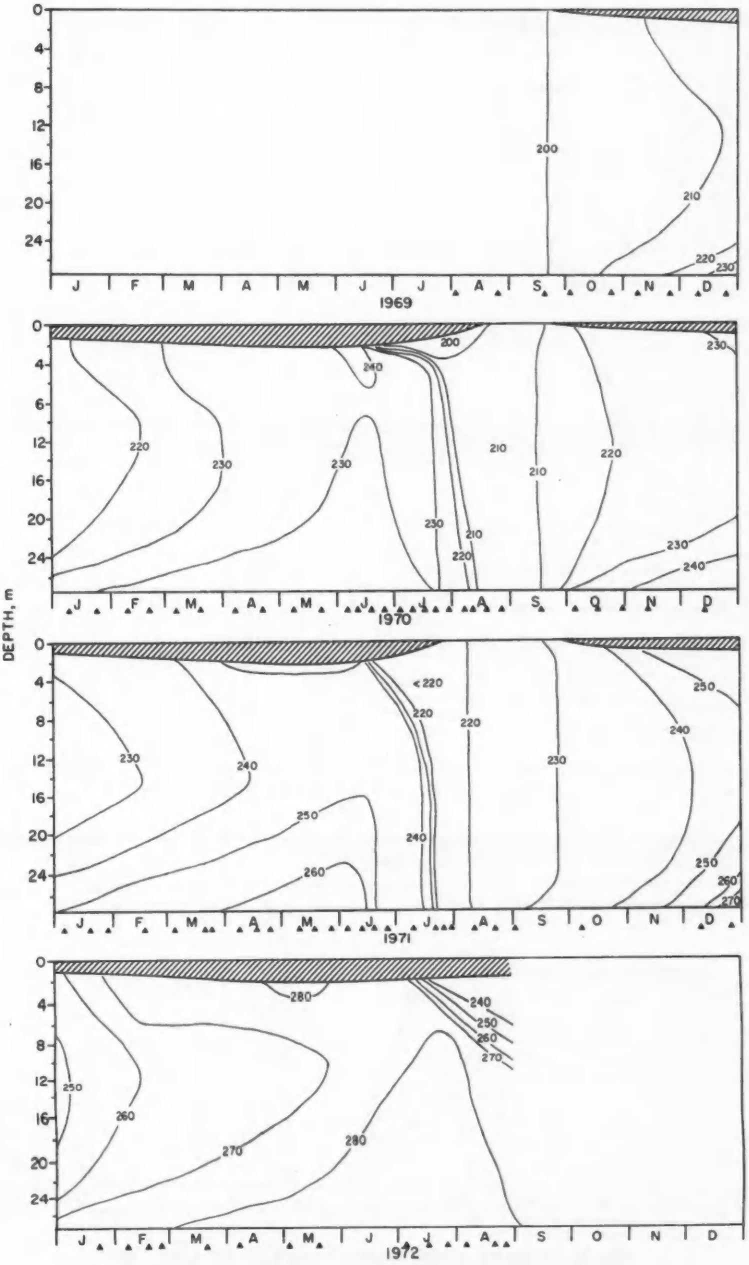


FIG. 7. Seasonal conductivity isopleths (μmho/cm²) for Char Lake.

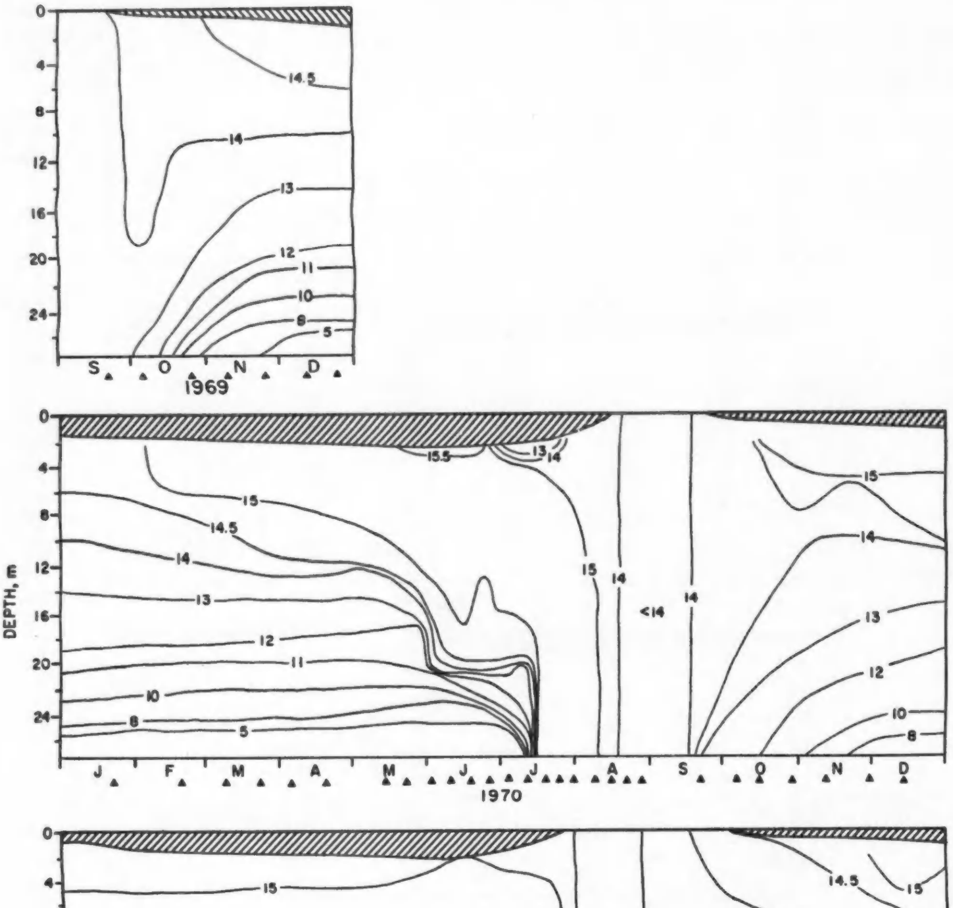


FIG. 8. Seasonal oxygen isopleths (mg/liter) for Char Lake.

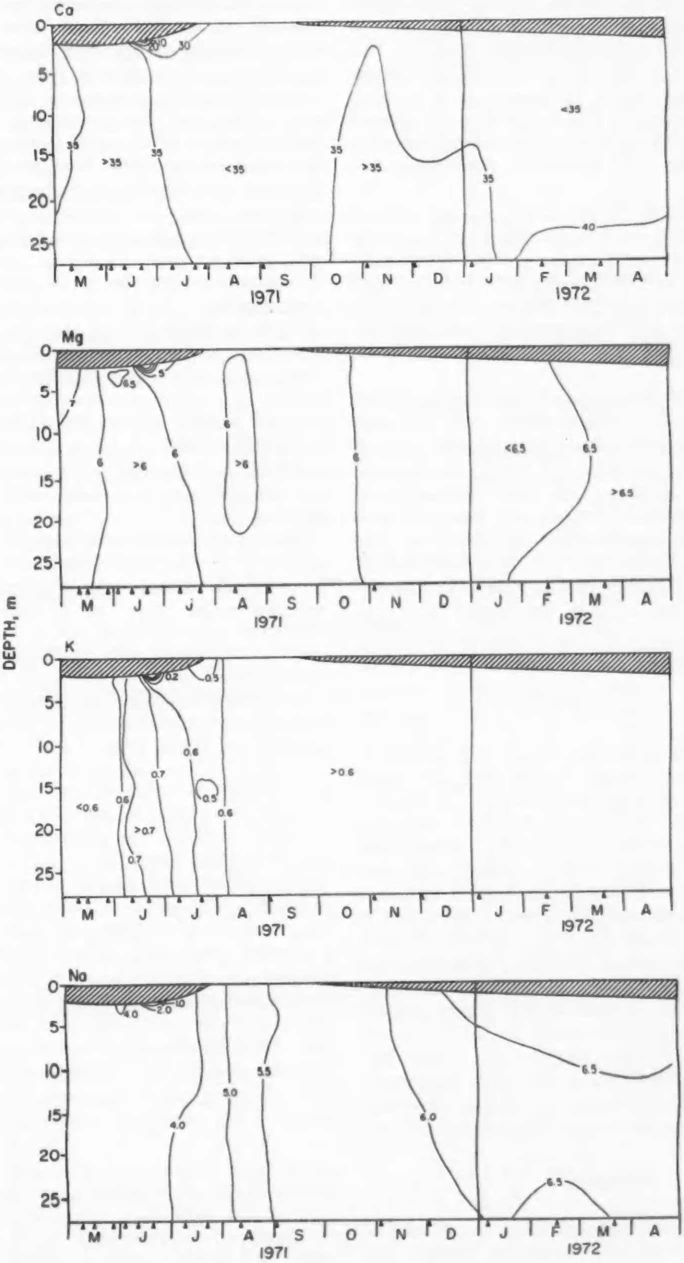


FIG. 9. Ca^{++}, Mg^{++}, Na^{+}, and K^{+} concentrations (mg/liter) in Char Lake, 1971–72.

found at 26 m. In spite of the extreme oligotrophic nature of the lake, winter oxygen depletion at the sediment surface was considerable, probably due to respiration by the benthic community (Welch 1974). The mean oxygen concentration of the lake was near saturation at fall turnover and increased slightly to over 15 mg/liter by the spring, reflecting the balance between freeze-out and respiration (Welch 1974).

Concentrations of Ca, Mg, and K reached maxima under late spring ice (Fig. 9). No such trend was apparent for sodium. Thawing ice and dilute meltwater entering the lake in June and early July caused depletion in major ions near the ice. Mixing of this dilute meltwater with deeper water during the ice-free period caused the overall concentration to decrease.

Chloride and bicarbonate had annual cycles similar to those of major cations, with the only large alteration being due to meltwater dilution under late spring ice (Fig. 10). Slight increases in concentrations of both ions were detected over winter near the lake bottom and near the lake surface, due to concentration by freeze-out (see below). Sulfate results were too variable to include seasonal data. Reliable results were not obtained during the summer of 1971, but ranged from 8 to 14 mg/liter during the winter. Two major ions, Na and Cl, appeared to show long-term changes as well as annual cycles. Both increased by approximately 40% from May 1971 to May 1972.

Soluble reactive phosphorus, which was measured only during the summer months, was consistently undetectable (<0.7 µg/liter). Ammonia nitrogen was also undetectable throughout the year (<2 µg/liter). Nitrate nitrogen increased above the sediments under late spring ice, and also entered the lake from meltwater (Fig. 11). The maximum concentration recorded during such periods was 30 µg/liter. During the ice-free season nitrate was undetectable.

Total dissolved phosphorus was near the lower limit of detection. Total dissolved nitrogen concentrations, although well within the range of the method, revealed no seasonal patterns (annual averages were 2 µg/liter for TDP and 75 µg/liter for TDN). Total dissolved iron was consistently undetectable (<1 µg/liter). Dissolved organic carbon was too low to be measured with certainty (<90 µg/liter).

Suspended phosphorus ranged from 1 to 5 µg/liter ($\bar{x} = 2$ µg/liter). Due to low concentrations, no seasonal patterns were discernable. Suspended nitrogen ranged from 7 to 27 µg/liter ($\bar{x} = 16$ µg/

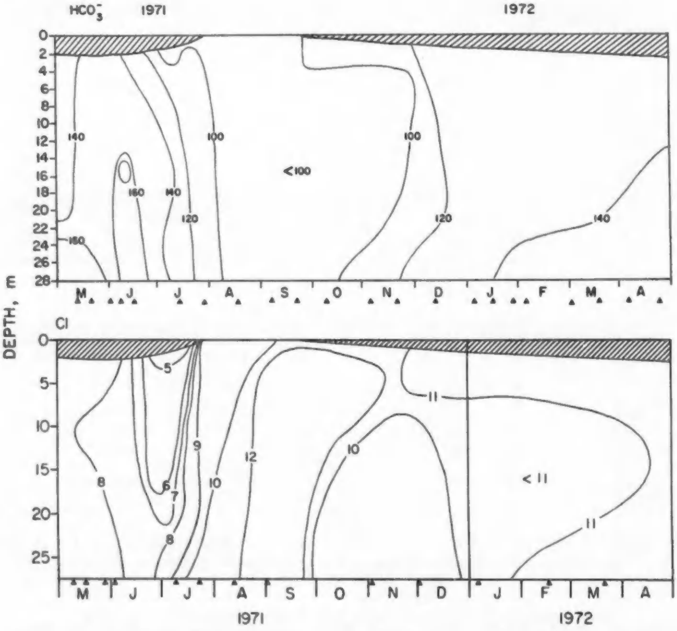


FIG. 10. HCO$_3^-$ and Cl$^-$ concentrations (mg/liter) in Char Lake, 1971–72.

liter). A slight seasonal trend was noticeable, with slight dilution under ice due to melting in June, followed by an increase in upper strata during July and August (Fig. 12a). This trend was even more noticeable with suspended carbon, which decreased in winter, and increased slightly under spring ice (Fig. 12b). The annual mean was 172 µg C/liter. Soluble reactive silica had the most pronounced annual cycle of any element. Dilution due to meltwater in spring was followed by a slight decrease during the open-water period, probably due to use by littoral and planktonic diatoms (Fig. 13). Concentrations increased considerably during winter.

Values for pH decreased slightly during winter, then increased with spring runoff (Fig. 14). The winter decrease was most likely due to addition of CO_2 to the lake by the benthic community. Calculations of partial pressure of this gas (pCO_2) based on pH, temperature, and alkalinity titrations indicate that the lake became somewhat supersaturated with respect to atmospheric equilibrium during winter, but returned to slightly above saturation during the ice-free period (Fig. 15), probably due largely to loss of CO_2 to the atmosphere.[6]

PRECIPITATION CHEMISTRY

Rain and snow in the Resolute area consistently contained low concentrations of phosphorus and nitrogen (Table 2). Other elements varied greatly from sample to sample, probably depending to a large degree on wind direction and velocity, and, in the case of snow, on how much a particular sample had been blown about.

When compared to relatively uncontaminated areas of southern Canada, Resolute precipitation is low in both phosphorus and nitrogen (Table 3). This is probably due to the small amount of terrestrial organic matter, frozen nature of the terrain, and, in the case of nitrogen, to the lack of thunderstorms in the area. The absence of industrial and agricultural activity in the arctic may also be a factor. Low natural input of nutrients via precipitation, rather than low temperatures, may cause arctic lakes to be low in productivity (Schindler et al. 1974).

Major ion concentrations in precipitation were higher than in the samples from southern Canada, probably because the latter were from the Precambrian Shield, where weathering is extremely slow and vegetation protects the substrates from wind. The proximity of Char Lake to the sea and to the Resolute airstrip may also be factors.

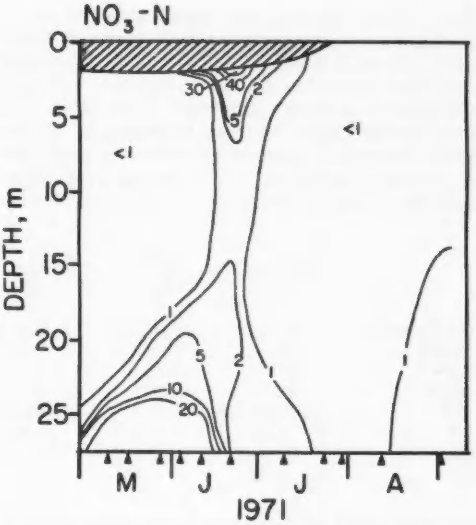


FIG. 11. Nitrate concentrations (µg/liter) in Char Lake, 1971.

INFLOWS

Inflows 2, 3, and 4 had lower concentrations of ammonia, but higher nitrate than precipitation (Table 4). The concentration of total dissolved nitrogen, however, was about equal to that in precipitation. Phosphorus appeared to be slightly less than in rain. Concentrations of major ions were, of course, much higher in runoff than in precipitation, due to solution from rock. Inflows 3 and 4 showed a general increase in conductivity during summer, inflow 2 conductivity was variable, probably because of the influence of inflow 1 nearby, and inflow 1 had conductivity values one to two orders of magnitude higher than 3 and 4. The significance of this result is discussed below. Our results show that the conductivity of the nearby Mecham River, draining about 100 km^2, also increased steadily during the summer.

Discussion

The fact that concentrations of most elements are highest both at the lake bottom and ice-water interface during winter appears at first glance to show that return from sediments and concentration by freeze-out are responsible for annual variation in chemical concentration. Comparison of the total mass of elements in the lake at the beginning and near the end of ice cover, however, indicates that freeze-out alone is responsible (mass of various ions in Char Lake near the beginning of winter and after several months of ice cover — conductivity is µmho/cm corrected for freeze-out and other data are in kilograms for the whole lake):

---

[6] Unpolluted lakes in free circulation with the atmosphere, appear to maintain pCO_2 values slightly above saturation (Schindler et al. 1974). This is probably due to the excess of CO_2 released by decomposition of autochthonous and allochthonous matter over consumption of CO_2 by photosynthesizing aquatic plants.

	Sept. 1, 1971	Mar. 19–21, 1972	% change
Conductivity	232	231	–0.4
HCO_3^-	588	586	–0.3
Ca^{+2}	167.7	169.4	+1.0
Mg^{+2}	30.7	29.8	–2.9
Na^+	29.8	29.9	+0.3
K^+	3.46	3.12	–9.8
Cl^-	66.7	50.4	–24.4
Si	1.26	1.28	+2.2

and that inputs of electrolytes from sediments over winter in Char Lake are negligible, in spite of the fact that the ionic composition of the interstitial water from the upper 15 cm of sediment is slightly higher than the average for lake bottom water over the year (Table 5).

Chloride deviated most from this pattern, with a 24% decrease from September to March. The long-term overall increase mentioned above appears to occur mainly during the summer months. Together these two observations suggest that the observed long-term changes in chloride are due to factors outside the lake. Without the summer influx the element would probably stabilize at a lower concentration.

The annual cycle of concentrations of all elements therefore appears to be affected largely, if not entirely, by freeze–thaw cycles. Roen (1962) also concluded that increases in conductivity beneath the ice of larger East Greenland lakes resulted from freeze-out, but Hansen (1967) disagreed; neither tested the hypothesis by making the necessary volume and concentration calculations. Hansen calculated that the conductivity increase in the upper water layers could result from freezeout, as the 1 C temperature gradient in the water column would be sufficient to maintain stratification, the concentrate "floating" beneath the ice. However, our data, showing an increase of conductivity below the ice and in deepest water, could

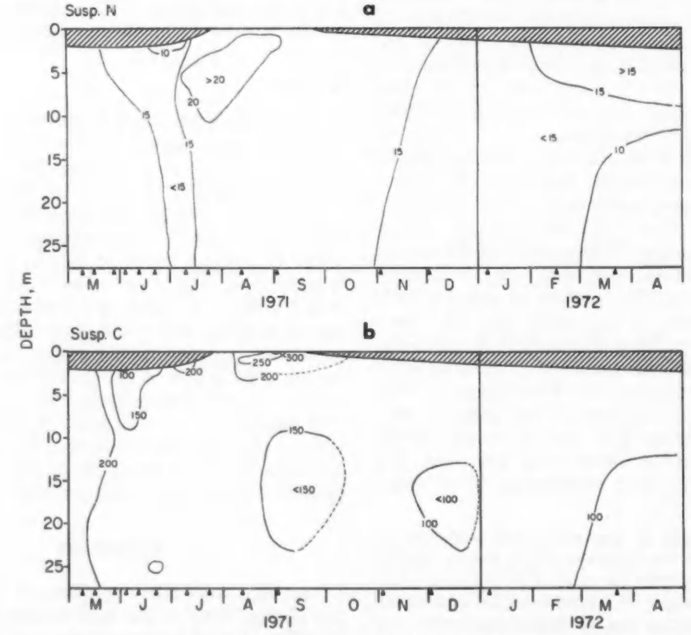


FIG. 12. Suspended a) nitrogen and b) carbon (µg/liter) in Char Lake, 1971–72.

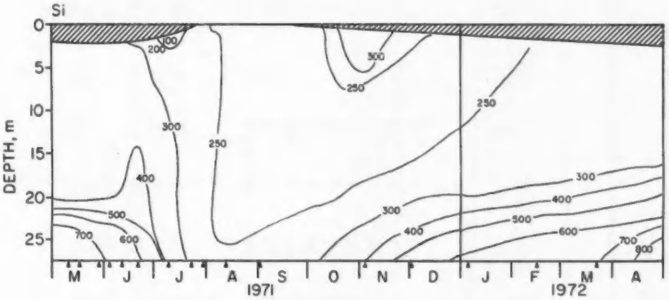


Fig. 13. Soluble reactive silicate (μg/liter) in Char Lake, 1971–72.

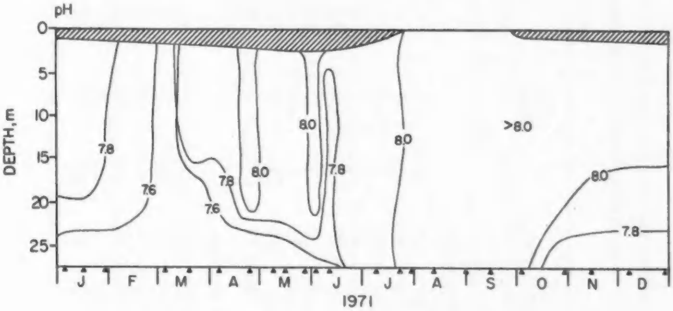


Fig. 14. pH values in Char Lake, 1971.

be explained by postulating sinking of solute-rich water originating from freeze-out. This might sink in vertical density currents of the type demonstrated by Bradley (1969), thus retaining its identity while sinking and slowly warming by absorbing heat from the surrounding water. As it contacted the bottom and continued to move deeper it might pick up silica from the sediments and come to rest in the deepest part of the lake.

The lake always has a higher mean conductivity than the inflowing streams (Fig. 7 and Table 4), which could be explained by postulating that some particulate inorganic matter dissolves after entering the lake. In addition, we offer the following scheme for concentration of dissolved elements: Early runoff flowing into the lake is low in solutes; in addition, melting ice and snow on the lake surface and margin combine to form a relatively dilute layer beneath the ice, which provides most of the outflow at the time of major runoff. High conductivity water deeper in the lake is unaffected. As the summer progresses, solutes in inflowing streams become more concentrated but at the same time their flow is greatly reduced. With the disappearance of the ice sheet the lake circulates and the outflow conductivity increases, becoming even higher than the inflows, but as this is after the period of major runoff the effect is small. After freezeup, cryoconcentration takes place and the cycle begins again the following spring. The net result is a steady state where the lake has a higher concentration of dissolved material than the average concentration in inflowing and outflowing stream waters (Fig. 16). This steady state appears to have been disrupted in recent years. In 1967 through 1969 and 1970, conductivity measurements were all 195–200 µmho/cm (Rigler 1972; this paper). Since late 1969, there has been a steady increase in conductivity, with latest values in 1972 ranging 240–280 µmho/cm

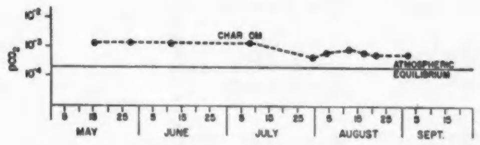


FIG. 15. Partial pressure of gaseous CO_2 in Char Lake, 1971. Values are for a depth of 1 m.

TABLE 2. Chemical components of precipitation chemistry in the Resolute area, 1971.

Date	mg/liter							µg/liter											
	Ca	Mg	Na	K	HCO_3	Cl	SO_4	NH_3– N	NO_3– N	TDN	Sol. react. P	TDP	Susp. C	Susp. N	Susp. P	Si	TD Fe	pH
								Snow samples										
May 13	1.46	0.51	0.44	0.55	–	–	–	14	144	283	1	3	–	–	–	0	–	–
June 3	2.50	0.44	0.35	0.07	11.1	–	–	8	48	124	1	3	560	51	3	23	–	6.2
June 8	1.48	0.52	0.26	0.04	11.4	–	–	6	29	88	<0.7	1	370	26	<1	18	–	6.2
June 12	1.88	0.92	0.82	0.08	–	5.0	4.6	17	45	131	2	4	20	19	1	3	–	–
June 12	1.02	0.38	1.32	0.12	2.1	11.9	0.9	6	37	158	<0.7	13	1162	59	2	6	–	6.2
June 12	0.44	0.10	0.26	0.07	0.9	0.3	0.9	8	2	80	13	18	460	26	3	7	–	5.9
June 12	5.17	1.47	3.88	0.36	–	17.0	5.4	6	31	83	<0.7	4	750	33	4	46	–	7.7
June 29	2.81	0.39	0.32	0.19	8.8	1.0	2.0	<1	118	237	1	3	1850	155	19	0	3	7.0
$\bar{x}$	2.09	0.59	0.96	0.18	6.9	7.0	2.8	8	57	148	2	6	739	53	5	13	3	6.5
								Rain samples										
July 20	11.1	1.14	1.40	0.21	31.6	2.9	2.7	22	290	481	21	19	4197	271	–	71	1	8.2
Aug. 4	6.5	0.53	0.21	0.10	19.0	5.5	1.0	251	91	399	2	3	4917	293	28	39	10	7.7
Aug. 7	72.6[a]	1.21	0.92	0.20	14.7	–	–	8	–	272	2	5	6954	326	35	42	–	7.5
Aug. 23	4.19	0.50	0.87	0.40	–	1.2	0.7	55	4	139	9	12	–	–	22	–	–	–
Aug. 24	3.37	0.25	0.67	0.09	–	1.1	0.4	22	3	40	2	11	13228	648	115	–	–	–
x	19.6	0.73	0.81	0.20	21.8	2.7	1.2	72	97	266	7	10	7144	384	50	51	6	7.8

[a] $\bar{x}$ is 6.29 without the indicated high value.

TABLE 3. A comparison of average chemical components of Resolute precipitation and samples from southern Canada.

	mg/liter						µg/liter					
	Ca	Mg	Na	K	NH_3–N	NO_3–N	TDP	Sol. react. P	TDN	Si	pH	Reference
						Snow						
Resolute area 1971–72	6.3	0.73	0.81	0.20	8	57	6	2	148	13	6.5	This study
Clear L., E. Ont. 1967–68	0.72	0.10	0.16	0.06	625	320	10	5	0	110	–	Schindler and Nighswander 1970
Exp. Lakes Area, 1970–71	0.35	0.07	0.35	0.09	39	206	6	4	311	0	5.0	Barica and Armstrong 1971
Exp. Lakes Area, 1971–72	0.53	0.12	0.27	0.24	461	588	161	140	190	–	–	D. W. Schindler (unpublished data)
						Rain						
Resolute area 1971–72	6.3	0.73	0.81	0.20	72	97	10	7	266	51	7.8	This study
Clear L., E. Ont. 1967	1.2	0.50	0.08	0.08	555	198	17	4	–	234	–	Schindler and Nighswander 1970
Exp. Lakes Area, 1971	0.43	0.13	0.25	0.12	187	169	17	6	–	370	–	D. W. Schindler (unpublished data)

TABLE 4. Chemical components of inflow and outflow streams in the Char Lake watershed.

	mg/liter								µg/liter										
Date	Ca	Mg	Na	K	Cl	SO$_4$	HCO$_3$	Conductivity (*µmho/cm*)	NH$_3$–N	NO$_3$–N	TDN	Sol. react. P	TDP	Susp. C	Susp. N	Susp. P	Si	TDFe	pH
								Inflow 1											
June 30	319	74	433	160	470	390	130.0	–	18	402	544	<0.7	3	221	13	1	610	1	8.0
July 20	78.2	31.2	192	9.93	332.5	152.5	131.5	1550	22	223	383	1	4	290	11	4	603	1	8.2
July 28	387	211	1450	810	2475	1450	124.7	9180	465	824	2170	1	87	541	11	4	791	1	7.9
Aug. 4	174	78.1	544	30.0	845	465	110.8	3880	99	696	1147	<0.7	4	645	–	4	669	3	7.9
Aug. 7	348	166	1250	77.0	1511	949	116.8	–	540	741	1870	1	7	127	9	1	792	1	7.7
Aug. 17	191	68.1	377	20.3	470	570	109.0	2960	53	475	724	<0.7	2	1246	41	9	628	3	8.0
Aug. 25	188	97.4	790	58.7	695	1120	–	5100	244	930	1538	1	5	1578	37	9	721	3	–
								Inflow 2											
June 18	57.0	15.4	51.1	4.77	–	–	92.1	–	<1	129	203	<0.7	3	1054	38	30	42	3	7.8
July 6	16.0	2.03	0.49	0.33	0.5	1.2	67.4	–	3	56	95	6	5	469	13	5	215	14	8.0
July 20	69.4	14.5	22.8	1.35	57.0	71.0	105.6	–	4	218	186	4	6	190	8	2	518	1	8.1
July 28	36.1	6.50	6.77	0.55	18.5	24.5	94.7	–	<1	141	187	2	5	591	37	6	346	4	8.1
Aug. 4	33.9	7.94	1.41	0.55	3.0	11.0	83.9	–	8	368	456	7	8	1670	–	26	325	39	7.9
Aug. 7	58.1	12.7	20.6	0.75	38.6	57.0	100.0	–	6	343	463	1	3	509	17	5	383	1	7.6
Aug. 25	33.8	6.62	6.11	0.60	8.0	23.0	–	–	4	290	303	<0.7	2	428	16	4	378	3	–
								Inflow 3											
June 18	57.0	15.4	51.1	4.77	–	–	92.1	–	<1	129	203	<0.7	3	1054	28	30	42	3	7.8
June 29	20.0	2.51	1.02	0.34	6.2	3.5	78.4	115	<1	1	57	1	3	–	–	–	244	4	8.0
July 6	24.3	3.35	1.21	0.91	1.2	1.8	97.0	120	<1	36	103	1	1	81	2	1	284	1	8.0
July 20	27.6	4.07	1.52	0.43	–	–	99.8	122	<1	66	135	<0.7	2	194	10	1	285	2	8.2
Aug. 7	48.4	12.6	4.33	0.50	–	–	111.0	190	7	188	284	<0.7	3	610	19	4	369	12	7.6
Aug. 16	36.2	6.37	3.99	0.47	7.0	20.0	115.0	dry	<1	264	324	<0.7	2	929	28	6	339	4	8.1
Aug. 25	34.1	6.04	3.53	0.49	6.0	14.5	–	dry	7	180	267	<0.7	2	182	12	9	407	4	–
								Inflow 4											
June 17	21.8	3.60	2.70	0.50	8.0	5.2	–	–	6	140	184	<0.7	4	170	10	13	351	6	–
June 18	21.9	3.53	3.24	0.51	8.9	5.5	79.7	–	<1	144	176	2	3	152	8	10	299	6	7.8
June 29	14.2	1.79	0.79	0.26	1.1	1.2	84.0	40	2	16	68	5	9	–	–	–	229	11	8.3
July 6	20.0	2.79	1.08	0.36	0.7	2.6	80.1	–	2	52	89	3	3	164	5	4	266	6	7.9
July 20	22.4	3.54	1.12	0.33	2.0	2.3	77.6	170	<1	26	78	3	3	195	11	2	212	8	8.0
July 28	27.0	4.31	2.06	0.39	4.5	13.0	79.9	220	<1	175	224	2	5	113	5	2	217	1	8.0
Aug. 4	30.6	6.16	2.42	0.66	4.8	8.4	125.9	190	3	280	373	5	6	6585	–	141	325	22	8.0
Aug. 7	34.7	5.78	2.63	0.47	6.0	13.2	95.0	260	<1	273	334	1	2	395	28	4	314	6	7.8
Aug. 25	28.2	5.28	2.09	0.60	–	–	–	230	3	219	246	<0.7	2	126	8	3	339	1	–
$\bar{x}$ (excl. inflow 1 see text)	33.6	6.64	8.4	0.91	10.1	15.5	93		2	158	219	2	4	442	15	8	293	9	7.9
								Outflow											
June 25	35.9	6.21	3.77	0.68	10.9	10.4	–	–	<1	<0.7	161	1	8	1750	127	6	335	3	–
June 29	16.9	2.80	2.48	0.41	2.6	4.9	63.6	125	<1	16	86	1	3	–	–	–	196	4	7.9
July 2	28.9	6.64	15.00	1.89	15.9	16.4	–	–	8	29	143	1	2	342	23	44	210	3	–
July 6	18.3	2.95	2.50	0.37	3.8	3.4	68.4	138	<1	13	71	1	2	314	26	2	179	1	7.9
July 20	31.9	5.48	3.98	0.62	9.5	6.0	114.2	218	<1	<0.7	60	1	2	130	10	2	272	<1	8.2
July 28	32.9	5.55	4.37	0.51	7.0	8.5	110.3	216	2	<0.7	71	<0.7	2	150	14	2	265	<1	8.1
Aug. 4	31.5	6.05	4.77	0.57	8.4	6.5	113.2	218	<1	2	64	1	3	232	–	3	273	1	8.1
Aug. 16	31.8	6.38	6.33	0.76	11.5	13.5	141.2	–	<1	25	100	2	1	130	5	1	202	3	7.9
Aug. 25	28.0	5.60	5.38	0.47	9.5	10.0	–	225	7	9	65	<0.7	1	134	13	1	254	<1	–
$\bar{x}$	28.5	5.30	5.40	0.70	8.8	8.8	101.8	190	2	10	91	1	3	398	31	8	243	2	8.0

(Fig. 7). This may reflect human disturbance in the watershed as mentioned in the introduction.

Inflow, which drains the area excavated for the airstrip, had extremely high conductivities and concentrations of Na and Cl, the factors observed to have long-term increases (Table 4). Concentrations of salts in streams early in the year, when water is supplied chiefly from snowmelt, are low (Table 4). Later in the summer there is a steady increase in concentration of electrolytes as meltwater sources move downward into the active layer. Increase in major ions would normally be ascribed to weathering of soils, because higher concentrations would be expected when decreased flow rates increase the contact time between water and weatherable materials. Weathering would not, however, explain the high concentration of nitrate (see especially stream 1, Table 4).

TABLE 5. Some chemical analyses of upper interstitial waters from Char Lake sediments, August 14, 1969. Representative chemical analyses of bottom lake water are given for the same date.

	Core		Lake	
	0–15 cm	15–30 cm	30–45 cm	25 m
Conductivity (*μmho/cm*)	235	295	310	195
Ca (*mg/liter*)	33.1	42.4	45.7	35.5
Mg	5.64	6.04	6.23	6.3
Na	3.14	3.30	2.81	3.0
K	1.51	1.74	1.51	0.64
Cl	8.04	8.93	8.15	7.0
pH	6.82	7.10	6.50	–

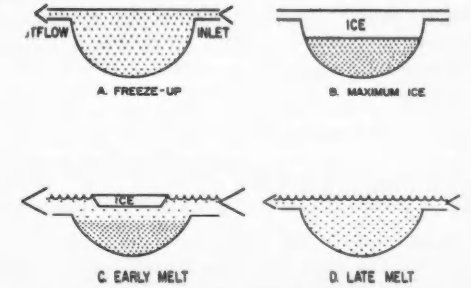


FIG. 16. How Char Lake remains more concentrated in electrolytes than its inflows. (Arrow heads indicate relative flow volume.) A, At freeze-up, inflow and outflow concentrations are slightly less than lake but flow volumes are low, so that dilution is negligible. B, During winter, inflows and outflow freeze solid. Electrolytes freeze out of ice, increasing concentration in lake water by about 20%. C, During early snow melt, flow volumes are high, but concentrations of electrolytes are low. The dilute meltwater flows as a layer over the deeper waters, where concentration took place during the winter. Ice remains on the lake, preventing it from mixing in the wind. As a result, excess solutes remain trapped in the deeper layers of the lake. D, During late melt, flow volumes decrease and electrolyte concentrations increase approaching conditions at freeze-up.

We propose the following mechanism: Nitrogen from precipitation (Table 2), and possibly also from fixation of atmospheric N_2 (Granhall and Selander 1973; Schell and Alexander 1973) is concentrated in terrestrial plants. As these decay, nitrate accumulates in the poorly drained active layer, to be concentrated downward by freezing in the fall, because refreezing of the active layer begins at the surface. This concentration mechanism would be similar to the freshening of sea ice, whereby solutes in the active zone are trapped as minute brine pockets and slowly melt down to permafrost, where they remain. This mechanism would explain the observed low nitrogen in upper arctic soils (Russell 1940; Sorensen 1941; Wilson 1966). If this effect is typical, disturbance of arctic soils by such activities as pipeline or road construction might cause greatly increased nutrient loads to downstream terrestrial and aquatic ecosystems, due to melting of permafrost in the manner observed in the area of inflow 1, as mentioned above.

THE ANNUAL LIGHT REGIME AND ITS EFFECT ON THE LAKE

The light regime of Char Lake is affected by two factors when the sun is above the horizon: snow cover and turbidity. Both are rather predictable, as the melt period affects both.

The data in Fig. 6, which shows the extinction coefficient of light in deeper waters, underestimate the contribution of meltwater to turbidity during June as turbid meltwater is then confined to a narrow band under the ice. Accurate coefficients of extinction were not obtained in this stratum because of errors due to surface light entering through the hole in the ice. Much higher turbidity was associated with "ice-out" in 1969, which occurred during a 2-day storm, resulting in high runoff of suspended sediments.

Although snow cover is thin and patchy on Char Lake, the polar night imposes an effect not unlike the winter in temperate latitudes, where 0.5–1.0 m of snow and turbid ice usually impose near total darkness for several months in winter. Whenever the sun is above the horizon, there is a measurable light input in Char Lake.

TABLE 6. Nutrient input to and output from Char Lake, calculated from 1971 chemistry and mean precipitation figures for the area. See text for details of output calculations. All data in kilograms unless otherwise specified.

	Precipitation direct to lake surface (*kg*)			ratio to Na	runoff	ratio to Na	input(s)	input, ratio to Na (formula 2)	output(O) (formula 1)	% O/I	% O/I (formula 3)
	rain	snow	total								
TDP	0.34	0.23	0.57	0.0083	2.01	0.00048	2.58	0.0014	1.69	65	<40
TDN	8.95	5.60	14.55	0.21	110.1	0.026	124.6	0.049	51.3	41	35
Ca	70.4	79.2	149.6	2.18	16896	4.0	17046	3.77	16064	94	140
Mg	19.9	22.3	42.2	0.61	3339	0.79	3381	0.76	2987	88	129
Na	32.3	36.4	68.7	1.00	4224	1.00	4293	1.00	3044	71	100
K	6.1	6.9	13.0	0.19	458	0.108	471	0.118	395	84	110
HCO_3	734	261	995	14.48	46766	11.07	47761	11.50	57382	120	164
Susp C	240	28	268	3.91	222	0.053	491	0.531	224	46	14
Susp N	12.9	20.1	33.0	0.48	7.5	0.0018	40.5	0.062	17.5	43	9
Susp P	1.68	0.19	1.87	0.027	4.0	0.00095	5.87	0.0041	4.51	76	37
Fe	0.20	0.11	0.31	0.0045	4.53	0.0011	4.84	0.00156	1.1	23	23
Cl	91	265	356	5.18	5079	1.20	5435	1.69	4960	91	96
SO_4	40	106	146	2.13	7794	1.85	7940	1.88	4960	62	87
Si	1.72	0.49	2.21	0.032	147.3	0.035	149.5	0.035	137.0	92	129

NUTRIENT INPUT

The input of phosphorus and nitrogen has been found to be a useful criterion of a lake's degree of trophy (Vollenweider 1968). His data are, however, largely for temperate eutrophic and mesotrophic lakes, and include no ultra-oligotrophic or arctic lakes. Even a crude estimate of nutrient input for Char Lake should therefore be of interest. Schindler and Nighswander (1970) give formulas based on precipitation, runoff, evaporation, and nutrient concentrations in precipitation and runoff. Using these formulas, and assuming that there is negligible evaporation and evapotranspiration, we calculate that the annual income of phosphorus for Char Lake is 0.016 g/m^2 per year and the annual nitrogen income is 0.314 g/m^2. These figures are the lowest we know of for any lake. They probably reflect the low atmospheric content of phosphorus and nitrogen as discussed above, as well as low terrestrial nitrogen fixation and geochemical weathering which would be expected in the arctic.

The average ratio of N:P entering the lake is 20:1 by weight. This is higher than the ratio believed to be needed for phytoplankton. Schindler et al. (1971, 1973, and unpublished data), in studying a lake with an N:P input of 16:1 by weight, found that the phytoplankton responded to additions of phosphorus rather than nitrogen. These results suggest that Char Lake would respond with increased production to additions of phosphorus, or phosphorus plus nitrogen, rather than nitrogen alone. Schindler et al. (1974) confirmed this conclusion with studies of water columns isolated with polyethylene film in Char Lake.

RETENTION BY THE LAKE

Measurements of water outflow were nearly impossible to make, since much water left the lake under and over ice on the outlet before the outlet thawed. In addition, the porous nature of the overburden near the outlet probably allowed some water to flow from the lake outside the main stream channel. Nevertheless, rough estimates of chemicals leaving the lake were calculated in two ways. In method 1, the formula used was:

$$(1) \qquad O = A_d\,(P - E_r) + A_o\,(P - E)$$

where O is the annual outflow in m^3, P, E_r and E are annual precipitation, evapotranspiration, and evaporation, respectively, and A_d and A_o are the terrestrial drainage area and lake surface area, respectively. E and E_r were both assumed equal to 15% of P. The outflow volume, O, was then multiplied by the average outflow concentration.

In the second method, the basis for calculation was elemental ratios. The ratio of each element in runoff and precipitation to Na was chosen as an index, because Na is a conservative element that does not form insoluble compounds, yet can be analyzed with good accuracy:

$$(2) \qquad 0.124\,(e_p/Na_p) + 0.876\,(e_R/Na_R) = R_I$$

$$(3) \qquad \text{then } (e_o/Na_o)/R_I = e_o \text{ as } \%\ e_I$$

where e is the concentration of each element in precipitation (subscript *p*), runoff (subscript R), and outflow (subscript *o*). R_I is the ratio of each element to Na in total inflow (subscript I). The constants 0.124 and 0.876 are the proportion of total inflow from precipitation and from runoff, respectively.

Whether based on formula (1) or (3), retention of entering phosphorus, nitrogen, suspended carbon, and iron by the lake is far higher than for other elements (Table 6). This undoubtedly reflects their participation in critical aspects of lake metabolism. The retention of phosphorus and nitrogen appears to be lower than in oligotrophic lakes from temperate North America (for example Schindler and Nighswander 1970; Schindler and Fee 1973; Schindler et al. 1973; Vollenweider 1968, Table 4). Some of the lakes listed by Vollenweider, and discussed by Hutchinson (1957, p. 845) have similar low retentions for these elements, but they are usually mesotrophic to eutrophic lakes. Mortimer (1939) concluded that less productive lakes in the English Lake District have lower nitrogen retention, which appears to contradict the above evidence. Detailed studies of water renewal, nitrogen fixation, and denitrification in a variety of water bodies are needed before a general conclusion can be drawn.

Acknowledgments

Special thanks are due to Dr F. H. Rigler for his advice and encouragement throughout the study, and for much helpful advice on the manuscript. Drs K. Patalas and A. L. Hamilton also read the manuscript. Much of the data analysis was done by V. E. Frost and P. Cross.

This paper is contribution No. 18 of the Char Lake Project and contribution No. 247 of the Canadian Committee for the International Biological Program. The research was supported by C.C.I.B.P. and the Fisheries and Marine Service.

ANDREWS, J. T., R. MCGHEE, AND L. MCKENZIE-POLLOCK. 1971. Comparison of elevations of archaeological sites and calculated sea levels in arctic Canada. Arctic 24: 216–228.

Arkay, K. 1972. Species distribution and biomass characteristics of the terrestrial vascular flora, Resolute, N.W.T. M.Sc. Thesis. McGill Univ. Montreal, Que. 146 p.

Armstrong, F. A. J. 1957. The iron content of sea water. J. Mar. Biol. Assoc. U.K. 36: 317–321.

Armstrong, F. A. J., and E. I. Butler. 1962. Chemical changes in sea water off Plymouth during 1960. J. Mar. Biol. Assoc. U.K. 42: 253–258.

Armstrong, F. A. J., and S. Tibbetts. 1968. Photochemical combustion of organic matter in sea water for nitrogen, phosphorus and carbon determination. J. Mar. Biol. Assoc. U.K. 48: 143–152.

Barica, J., and F. A. J. Armstrong. 1971. Contribution by snow to the nutrient budget of some small northwest Ontario lakes. Limnol. Oceanogr. 16: 891–899.

Barr, W. 1971. Postglacial isostatic movement in northeastern Devon Island: a reappraisal. Arctic 24: 249–268.

Bendschneider, K., and R. J. Robinson. 1952. A new spectrophotometric method for the determination of nitrite in sea water. J. Mar. Res. 11: 87–96.

Bradley, W. H. 1969. Vertical density currents — II. Limnol. Oceanogr. 14: 1–3.

Brewer, M. 1958. The thermal regime of an arctic lake. Trans. Am. Geophys. Union 39: 278–284.

Brunskill, G. J., D. Povoledo, B. W. Graham, and M. P. Stainton. 1971. Chemistry of surface sediments of sixteen lakes in the Experimental Lakes Area, northwestern Ontario. J. Fish. Res. Board Can. 28: 277–294.

Carpenter, J. H. 1965. The Chesapeake Bay Institute technique for the Winkler dissolved oxygen method. Limnol. Oceanogr. 10: 141–143.

Forel, F. A. 1892. La thermique des lacs l'eau douce. Verh. Schweiz. Naturforsch. Ges. 75: 5–8.

Granhall, U., and H. Selander. 1973. Nitrogen fixation in a subartic mire. Oikos 24: 8–15.

Hagglund, M. 1958. Climate of Cornwallis Island, p. 21–26. *In* R. Thornsteinsson [ed.] Cornwallis and Little Cornwallis Island, District of Franklin N.W.T. Geol. Surv. Can. Mem. 294: 134 p.

Hansen, K. 1967. The general limnology of arctic lakes as illustrated by examples from Greenland. Medd. Grønland 178(3): 77 p.

Hill, H. 1967. A note on temperatures and water conditions beneath lake ice in spring. Limnol. Oceanogr. 12: 550–552.

Hobbie, J. 1973. Arctic limnology: a review. *In* M. Britton [ed.] Alaskan Arctic Tundra. Arct. Inst. N. Am. Tech. Pap. 25 (In press)

Hutchinson, G. E. 1957. A treatise on limnology. Vol. I. Geography, physics and chemistry. John Wiley and Sons, New York, N.Y. 1015 p.

Larson, D. W. 1972. Temperature, transparency and phytoplankton productivity in Crater Lake, Oregon. Limnol. Oceanogr. 17: 410–417.

Mackereth, F. J. H. 1955. Rapid micro-estimation of the major anions of freshwater. Proc. Soc. Water Treat. Exam. 4: 27–42.

1969. A short corer for subaqueous deposits. Limnol. Oceanogr. 14: 145–151.

McCann, S. B., P. J. Howarth, and J. G. Cogley. 1972. Fluvial processes in a periglacial environment. Trans. Inst. Br. Geogr. 55: 69–82.

Mortimer, C. H. 1939. The work of the Freshwater Biological Assoc. of Great Britain in regard to water supplies. The nitrogen balance of large bodies of water. Br. Waterw. Assoc. Off. Circ. 21: 1–10.

Murphy, J., and J. P. Riley. 1962. A modified single solution method for the determination of phosphate in natural waters. An. Chim. Acta 27: 31–36.

Reeburgh, W. S. 1967. An improved interstitial water sampler. Limnol. Oceanogr. 12: 163–165.

Rigler, F. H. 1972. The Char Lake Project: a study of energy flow in a high Arctic lake, p. 287–300. *In* Kajak and A. Hillbrecht-Ilkowska [ed.] Productivity problems of freshwaters. Polish Scientific Publishers, Warsaw. 918 p.

Roen, U. I. 1962 Studies on freshwater Entomostraca in Greenland II. Localities, ecology, and geophysical distribution of the species. Medd. Grønland 170(2): 249 p.

Russell, R. S. 1940. Physiological and ecological studies on an Arctic vegetation. II. The development of vegetation in relation to nitrogen supply and soil micro-organisms on Jan Mayen Island. J. Ecol. 28: 269–288.

Schell, D. M., and V. Alexander. 1973. Nitrogen fixation in arctic coastal tundra in relation to vegetation and micro-relief. Arctic 26: 130–137.

Schindler, D. W., F. A. J. Armstrong, S. K. Holmgren, and G. J. Brunskill. 1971. Eutrophication of lake 227, Experimental Lakes Area, northwestern Ontario, by addition of phosphate and nitrate. J. Fish. Res. Board Can. 28: 1763–1782.

Schindler, D. W., and E. J. Fee. 1973. The roles of nutrient cycling and radiant energy in aquatic communities. Proc. IBP Symp. on the Role of CO_2 and Radiant Energy in Aquatic Ecosystems, Aberystwyth, Wales, April 1973.

Schindler, D. W., J. Kalff, H. E. Welch, H. Kling, G. J. Brunskill, and N. Kritsch. 1974. Eutrophication in the high arctic: Meretta Lake, Cornwallis Island (75°N. Lat.). J. Fish. Res. Board Can. 31: (This issue).

Schindler, D. W., H. Kling, R. V. Schmidt, J. Prokopowich, V. E. Frost, R. A. Reid, and M. Capel. 1973. Eutrophication of lake 227 by addition of phosphate and nitrate: the second, third, and fourth years of enrichment, 1970, 1971, and 1972. J. Fish. Res. Board Can. 30: 1415–1440.

Schindler, D. W., D. R. S. Lean, and E. J. Fee. 1974. Nutrient cycling in freshwater ecosystems. *In* D. E. Reichle [ed.] Proc. IBP Symposium on Productivity of World Ecosystems, Seattle, Washington, September 1972. (In press)

Schindler, D. W., and J. E. Nighswander. 1970. Nutrient supply and primary production in Clear Lake, eastern Ontario. J. Fish. Res. Board Can. 27: 2009–2036.

SHAW, J. B. 1962. Ice survey Knob Lake 1961–1962: a critical re-evaluation of main environmental factors of lake ice growth. McGill Subarct. Res. Lab. Annu. Rep. 1961–1962: 34–61.

SOLORZANO, L. 1969. Determination of ammonia in natural waters by the phenolhypochlorite method. Limnol. Oceanogr. 14: 799–801.

SØRENSEN, T. 1941. Temperature relations and phenology of the northeast Greenland flowering plants. Medd. Grøn. 125: 1–305.

STAINTON, M. P. 1973. A syringe gas-stripping procedure for gas-chromatographic determination of dissolved inorganic and organic carbon in fresh water and carbonates in sediments. J. Fish. Res. Board Can. 30: 1441–1445.

VOLLENWEIDER, R. A. 1968. The scientific basis of lake and stream eutrophication, with particular reference to phosphorus and nitrogen as eutrophication factors. Organ. Econ. Coop. Dev. Paris (DAS/CSI/68) Tech. Rep. 27: 1–182.

WELCH, H. E. 1974. Metabolic rates of high arctic lakes. Limnol. Oceanogr. 19.

WILSON, J. W. 1966. An analysis of plant growth and its controls in Arctic environments. N.S. Ann. Bot. 30: 383–402.

WOOD, E. D., F. A. J. ARMSTRONG, AND F. A. RICHARDS. 1967. Determination of nitrate in sea water by cadmium–copper reduction to nitrite. J. Mar. Biol. Assoc. U.K. 47: 23–31.

Benthic Photosynthesis and Respiration in Char Lake[1,2]

H. E. WELCH[3]

Department of Zoology, University of Toronto, Toronto, Ont.

AND J. KALFF

Department of Biology, McGill University, Montreal, Que.

WELCH, H. E., AND J. KALFF. 1974. Benthic photosynthesis and respiration in Char Lake. J. Fish. Res. Board Can. 31: 609–620.

Benthic photosynthesis and respiration was measured by in situ oxygen change and correlated with in situ radiation in ultraoligotrophic Char Lake (lat. 74°42′N). Photosynthesis by the moss and deep sediment zones was correlated with light but photosynthesis by the shallow rocky zone was not. Total benthic gross photosynthesis in Char Lake is 47.5 g O_2 m^{-2} yr^{-1}, or 80% of the total lake photosynthesis. Benthic respiration was 43.6 g O_2 m^{-2} yr^{-1}, in close agreement with the 40.1 g O_2 m^{-2} yr^{-1} derived from whole lake metabolism. Light input is strongly dependent on snow cover and extinction coefficient. Subsurface irradiance is 24% of the photosynthetically available surface radiation.

WELCH, H. E., AND J. KALFF. 1974. Benthic photosynthesis and respiration in Char Lake. J. Fish. Res. Board Can. 31: 609–620.

Nous avons mesuré la photosynthèse benthique et la respiration à partir de la variation de l'oxygène in situ et avons établi une corrélation avec la radiation in situ dans le lac ultra-oligotrophe Char (lat. 74°42′N). Nous avons trouvé une relation entre la photosynthèse près des zones de mousse et de sédiment profond, mais non pour la photosynthèse près de la zone rocheuse peu profonde. La photosynthèse brute benthique totale dans le lac Char est de 47.5 gO_2 m^2 an^{-1}, soit 80% de la photosynthèse totale du lac. La respiration benthique est de 43.6 gO_2 m^{-2} an^{-1}, ce qui se rapproche de la valeur de 40.1 gO_2 m^{-2} an^{-1} obtenue pour la métabolisme du lac entier. L'apport de lumière dépend fortement de la couverture de neige et du coefficient d'extinction. L'irradiance au-dessous de la surface est de 24% de la radiation de surface disponible pour la photosynthèse.

Accepted January 21, 1974

THE IBP Char Lake Project, an attempt to measure energy flow and production processes in a high arctic lake, has been described by Rigler (1970) and the physical–chemical limnology of Char Lake given by Schindler et al. (1974). The estimation of primary production, a major portion of this work, is composed of three parts: the measurement of phytoplankton photosynthesis using C^{14} uptake, the measurement of benthic photosynthesis using C^{14} uptake, and the measurement of benthic photosynthesis using oxygen exchange. The benthic oxygen work only is reported in this paper.

Methods

The strategy used to estimate annual benthic photosynthesis was to obtain simultaneous measurements of light and photosynthesis for various bottom types, then reconstruct the annual light regime and predict production from the light:photosynthesis relation. The annual light regime was obtained by integrating daily total surface radiation with snow and ice cover, albedo, and extinction coefficient to give total irradiance received at each meter depth for 1970–72. Instrumentation and calculation of extinction coefficients are described in Schindler et al. (1974). Note that we have taken the photosynthetically available energy of natural daylight radiation to be 50% of the total, and all surface irradiances discussed below are half the total energy actually received.

---

[1] This paper, part of a special issue that comprises a comprehensive review of Limnology in Canada, was prepared to mark the 19th Congress of the International Association of Limnology (SIL), in Winnipeg, Man., during August 1974.

[2] Contribution No. 248 of CCIBP and contribution No. 19 of the Char Lake Project.

[3] Present address: Department of the Environment, Fisheries and Marine Service, Biological Station, St. Andrews, N.B.

Printed in Canada (J3290)

LIGHT

Measurement of light transmission through the spring snowpack in April and May, 1973 were made by tunnelling into snowdrifts with horizontal upper surfaces, sealing the entrance, digging a small hole upwards which was large enough to take the sensing head of a GM photometer, and making polychromatic light measurements as the underside of the snow was shaved away. Surface light was monitored with a deck cell and results expressed as percent surface radiation.

We also measured transmission through snow and ice in Char Lake and nearby Resolute Lake in spring by cutting two holes, 30 m apart, in areas of uniform snow cover, stretching lines between them above and below the ice surface, and having a diver make light measurements at 1-m intervals by holding the photometer against the sub-ice surface. Snow cover and surface radiation were simultaneously measured above the ice.

The results of the snow and light measurements (Fig. 1 and **Results**) show that light transmission in snow does not follow Lambert's law (see **Discussion**) and no simple model fits the data, so the hand-drawn curve in Fig. 1 was used to predict light transmission through snow. Because light extinction in snow is nearer an exponential than a linear process, and the snow cover on Char Lake is strongly drifted with

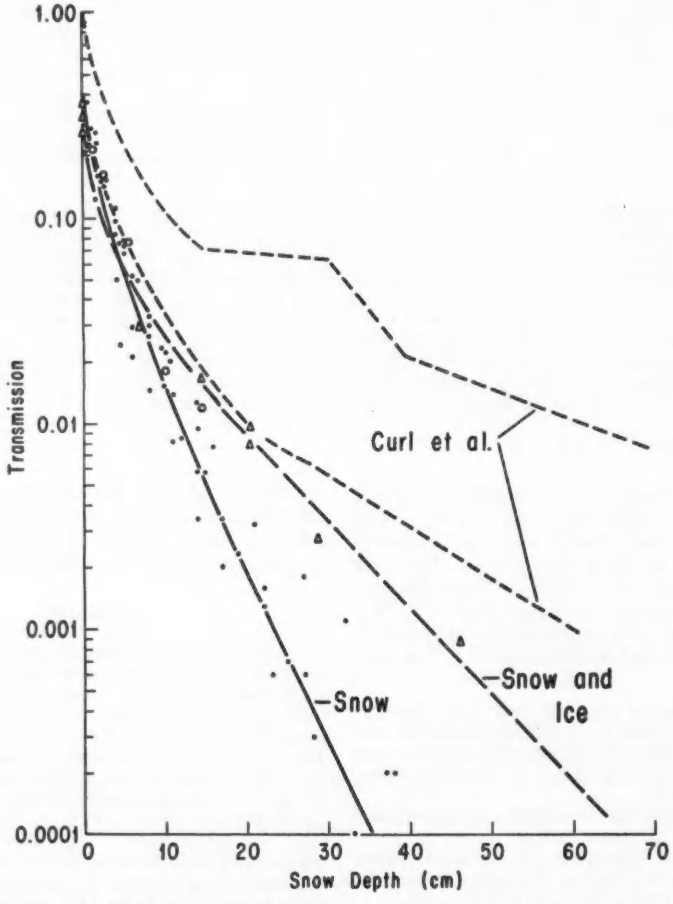


FIG. 1. Transmission of incident light trough snow and ice. ○ = Hand and Lundquist (1942), transmission through snow; ● = this study, transmission through snow; △ = this study, transmission through snow underlain by about 2 m of clear ice.

mean snow cover of about 8 cm including snow depths of 0–50 cm, using average snow cover for light-penetration calculations greatly underestimates light penetration. We therefore calculated transmission for individual snow-thickness measurements and averaged the light. Snow thickness was measured 24 times during the light periods of 1969–72, at 11 fixed stations on the lake.

We used K = 0.05 for transmission through clear black ice, as the transparency of clear ice is about the same as for pure water (Ruttner 1963, p. 23). We used 50% as the transmission through candled ice from the time the snow melted to the disappearance of the ice sheet, based on direct sub-ice measurements by diver and on light extinction curves extrapolated back to the surface. Most of this is albedo loss. We used 70% transmission into open water (albedo = 30%), again based on light extinction curves extrapolated back to the surface.

BENTHIC METABOLISM

Benthic gross photosynthesis and respiration was measured in July and August 1971, and April–August 1972, using diver-placed in situ chambers at various places about the lake. The five substrate types recognized and the chambers and techniques used on them were:

1. Rocky zone, 0–3 m. Flat rocks were carefully removed with forceps or tongs and placed in 485-ml glass ointment jars with plexiglass screwtops in which a small hole filled with silicone rubber cement had been placed. After sampling (see below), the area of exposed upper rock surface was measured by fitting Saran® film over the rock, cutting along the algal-covered surface, and weighing the plastic film. Rock volumes were also measured and subtracted from chamber volumes. Results were expressed as oxygen change per unit area of exposed rock surface.
2. Shallow sediment zone, 3–4 m. This is an extension of the rocky zone and is an area of silt accumulation below the zone of ice formation. The sediment is shallow, overlying rock, and is covered with green filamentous algae and diatoms. Plexiglass chambers of 1940 ml volume and 19.5 cm diameter with hinged lids were placed into the substrate, the lid was closed and held in place with rubber bands, and samples withdrawn through a rubber-filled hole in the lid. The contents were stirred gently before sampling by turning the propeller shaft that projected through the lid. Results were calculated on the basis of the area of the chamber, and the chamber volume above the substrate.
3. Moss zone, 3–19 m. The chambers used were similar to the above but were deeper (19.5 cm diameter; 3731 ml and 7462 ml in 1971, 6122 ml in 1972). The chambers were carefully pressed into the moss just deeply enough to seal the edges, then the lid was closed. Calculations were based on the whole chamber volume, as the dried moss volume in the chamber was negligible, and any oxygen change must therefore apply to virtually the entire chamber volume. The distribution of moss in Char Lake is shown in Fig. 2 and Table 1.
4. Moss "patches," or bare depressions in the moss zone (Fig. 2). A few measurements were made with the moss chambers as described below for sediment.
5. Deep sediment zone, the area below the moss zone. This was sampled with the moss chambers and calculations were based on the volume above the sediment surface. In these and other determinations we placed the chambers carefully so that there was negligible pressure-wave effect, and the surface inside the chamber was undisturbed; considerable practice was required before the divers could perform this task well. Also in the sediment zone, plexiglass tubes of 5.0 cm diameter were pressed into the substrate by diver, stoppered, and returned to a darkened water bath at 1.5 or 2.0 C in the laboratory, where oxygen consumption was measured on samples drawn at intervals by syringe.

After placement and stirring of the in situ chambers, the diver drew a water sample with a 10-cm^3 plastic syringe fitted with an 18 gauge needle which was inserted through the rubber-filled hole in the lid. The syringes were kept cold, returned to the laboratory within 45 min, and the oxygen concentration measured on a Radiometer blood–gas analyzer, the thermostated cell and electrode being kept in an ice bath. Calibration before and after a run was made by injecting water of known oxygen content, as determined by titration (Carpenter 1965).

The experiments usually ran 24 h; runs between 6 and 72 h long showed that metabolic rates were independent of experimental duration, provided the oxygen concentration in the chambers did not drop too low.

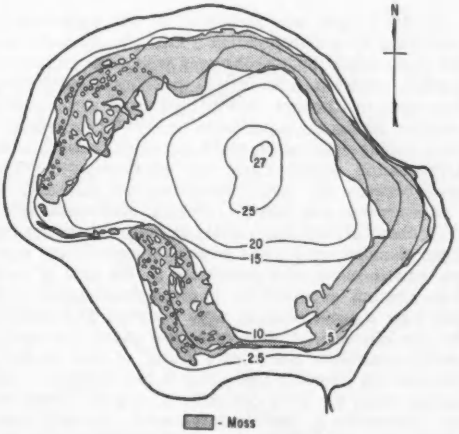


FIG. 2. Char Lake, showing bottom contours and moss distribution.

TABLE 1. Moss and nonmoss areas in Char Lake.

Stratum (*m*)	Moss (*ha*)	Nonmoss (*ha*)
0–1	0.00	5.41
1–2	0.00	4.89
2–3	0.29	3.00
3–4	0.75	2.15
4–5	1.07	0.95
5–6	1.88	0.30
6–7	2.04	0.25
7–8	1.31	0.25
8–9	1.29	0.74
9–10	0.85	0.81
10–11	0.68	1.03
11–12	0.73	1.57
12–13	0.44	1.35
13–14	0.45	1.75
14–15	0.33	1.55
15–16	0.18	0.99
16–17	0.13	0.86
17–18	0.11	0.90
18–19	0.06	0.89
19–20	0.00	1.09
20–21	0.00	1.55
21–22	0.00	1.74
22–23	0.00	1.51
23–24	0.00	1.78
24–25	0.00	1.02
25–26	0.00	0.67
26–27	0.00	0.86
27–27.5	0.00	0.14
Total	12.59	40.00

In 1972 light was measured at the experimental chambers by a diver holding a GM photometer, read on the surface by an observer who also monitored surface radiation. The portion reaching the chambers was used to calculate in situ light from surface light received during the experiment. In 1971 all experiments were during open water, and light was calculated from transmission curves. There was no detectable difference between the results from the two methods.

Respiration was taken as oxygen consumed in the dark chamber, and when added to oxygen change in the light chamber gave gross photosynthesis. These rates per square meter were multiplied by the area of each 1-m stratum occupied by a given community, then the total oxygen changes were summed and divided by the lake area. Unless otherwise stated, all results are in quantities per square meter of lake surface. Because the intensive study period ran from fall 1969 to fall 1972, the 1972 calculations include September 20 – November 1, 1969 light and snow data to present a complete year. The amount of photosynthesis occurring after freeze-up is only a small percentage of the annual total.

Results

LIGHT

The actual radiation received at Resolute is close to the maximum possible until the onset of temperatures above –15 C in early May (Fig. 3). Peak radiation is received in late May and early June and declines steadily thereafter, because of increased cloud cover, although this pattern is quite variable from year to year. Average radiation in late August and September is only 1/2–1/3 of the maximum possible. Total surface radiation is 4.0×10^5 kcal m^{-2} yr^{-1} with little difference between years (Table 2). In contrast to the seasonal pattern at the surface, only 7.0% of the 0.95×10^5 kcal m^{-2} yr^{-1} (24% of surface radiation) annually entering the water penetrates during February – June 15, 13.8% enters after September 1, and 79.2% enters June 15 – August 31. Snow cover sharply limits light penetration, contributing to the 2× difference found between years (Table 2), but in years with warm springs (1971) when snow melts early, turbidity tends to be high. Hence radiation received at 10 m is less variable (14%) between years than is radiation penetrating the water. In 1972 the ice did not leave the lake, but turbidity due to runoff was also low (Schindler et al. 1974), and the light received at 25 m was the highest of all 3 yr.

BENTHIC RESPIRATION

There was no correlation of respiration rate with year (except for rocky zone — see below), location around the lake, length of experiment, depth within a zone, time of year, or radiation. The respiration rate of the moss zone, 10.09 mg O_2 m^{-2} h^{-1} (N = 223; SE = 0.54), was much higher than that of the rocky or deep sediment zones (Table 3). The shallow sediment zone averaged 4.3 mg O_2 m^{-2} h^{-1} (N = 16; SE = 1.42), not significantly different from the rock measurements (N = 308), so the mean rate of 4.07 mg O_2 m^{-2} h^{-1} (N = 324; SE = 0.44), for both rock and shallow sediment was used for the shallow nonmoss area. The mean respiration rate for sediment cores from 10–24 m was 3.77 mg m^{-2} h^{-1} (N = 103; SE = 0.14). A few in situ chamber experiments gave similar results. Two sets of sediment cores (N = 14) from 6 m gave 10.8 mg O_2 m^{-2} h^{-1}. We therefore used 7 m as an arbitrary cutoff, with nonmoss below that respiring at 3.77 mg m^{-2} h^{-1} and nonmoss between 4 and 7 m respiring at the moss rate of 10.09 mg m^{-2} h^{-1}. The error due to arbitrary selection of nonmoss respiration rates in the 4–10 m zone is slight because most of this area is covered with moss (Table 1).

Calculations of rocky zone respiration rate used the ice-free area of bottom, and we assumed that on

June 15 the bottom surface beneath the ice was liquified and respiring; absorption of radiation by the bottom gives temperatures over 0 C by this time (D. Andrews, Department of Zoology, University of Toronto, Toronto, Ont., personal communication).

Total benthic respiration by these measurements is therefore 43.6 g O_2 m^{-2} yr^{-1} in Char Lake, of which the moss zone contributes 48%, the sediment zone 36%, and the rocky zone 16% (Table 3). This is close to the 40.1 g O_2 m^{-2} yr^{-1} respiration rate derived for the whole lake from winter oxygen curves (Welch 1974).

BENTHIC PHOTOSYNTHESIS

The rocky and shallow sediment measurements showed no correlation between gross photosynthesis and light over a range of 0.5–75 kcal m^{-2} h^{-1}. The mean photosynthetic rate was 10.44 mg O_2 m^{-2} h^{-1} (N = 315; SE = 0.54) with no difference between years, depths, lake location, or time of year. This rate was used down to *in situ* light levels of 3.55 kcal m^{-2} h^{-1}, at which point the moss equation (below) was used. The maximum rate applied during most of the photosynthetic season from June to October.

Moss photosynthesis (N = 216) was strongly correlated with light below 15 kcal m^{-2} h^{-1}, with no difference between moss and deep sediment photosynthetic rates (N = 7; 10–22 m), so the two data sets were used together. Between 15 and 50 kcal m^{-2} h^{-1} the photosynthetic response was highly variable and not correlated with light. Of 223 observations, elimination of those above 15 kcal m^{-2} h^{-1} leaves 191, where:

$$\text{gross photosynthesis (mg } O_2 \text{ } m^{-2} \text{ } h^{-1}) = 4.22 + 2.47 \text{ (kcal } m^{-2} \text{ } h^{-1}) \text{ SE for estimate} = 12.47 \quad (1)$$

We assumed that gross photosynthesis became zero at zero light, necessary for calculation purposes because during much of the year there is no light reaching the moss, so we used the relationship:

$$\text{gross photosynthesis (mg } O_2 \text{ } m^{-2} \text{ } h^{-1}) = 2.9374 \text{ (kcal } m^{-2} \text{ } h^{-1}) \text{ SE for estimate} = 15.2 \quad (2)$$

up to 15 kcal m^{-2} h^{-1}, at which point a constant rate of 44.06 mg O_2 m^{-2} h^{-1} was used. Over 15 kcal m^{-2} h^{-1} reached most of the moss zone in July and August.

We assumed that nonmoss below 7 m photosynthesized at the moss rate (supported by experimental data below 10 m) and that nonmoss above 7 m photosynthesized at the rocky–shallow sediment rate (supported by data down to 4 m). The

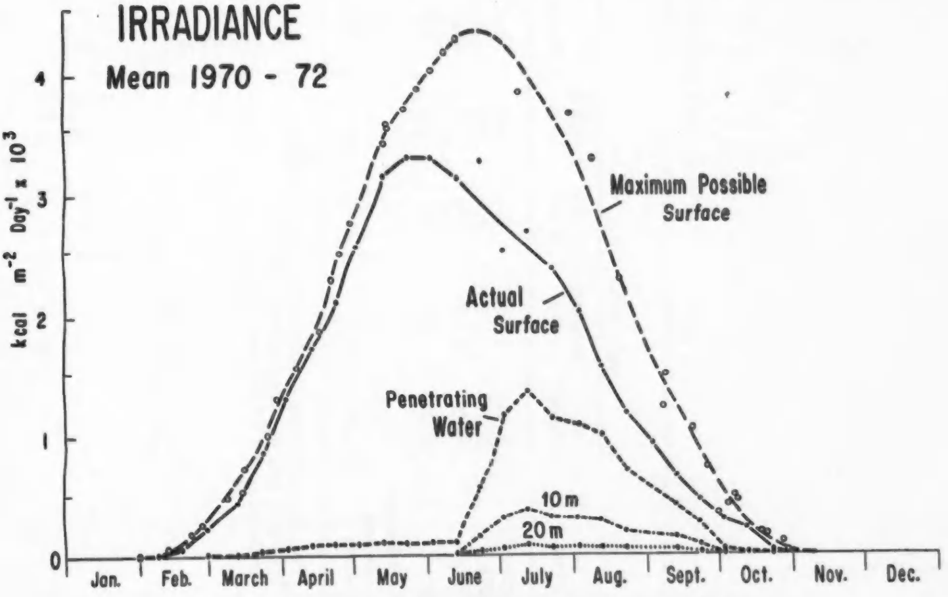


FIG. 3. Photosynthetically available irradiance at Char Lake.

TABLE 2. Light and benthic gross photosynthesis in Char Lake.

Year	Light, kcal $m^{-2} \times 10^5$				Annual gross photosynthesis, g O_2 m^{-2}				Spring[a] gross photosynthesis			
	At surface[b]	Entering water	Reaching 10 m	Reaching 25 m	Rocky[c]	Nonmoss	Moss	Total	Nonmoss	Moss	Total	% Annual total
1970	4.14	1.01	.24	.002	9.7	23.7	23.9	47.6	6.5	5.2	11.7	25%
1971	3.91	1.22	.28	.003	11.4	26.8	23.8	50.6	4.3	3.1	7.4	15%
1972	3.96	0.63	.24	.004	7.6	22.7	21.5	44.2	1.7	1.1	2.8	6%
Mean	4.00	.95	.25	.003	9.6	24.4	23.1	47.5	4.2	3.1	7.3	15%
% difference between years	5.5	49	14	38	33	15	10	13	74	79	76	76

[a] February to the day of snow melt, about mid-June.
[b] Given as 50% of total irradiance (see text).
[c] Included as part of nonmoss column.

possible error is minor because the 4–10 m zone is largely moss (Table 1). Annual benthic gross photosynthesis is therefore 47.5 g O_2 m^{-2} yr^{-1} (Table 2), with a 13% difference between the 3 yr. Of this, the moss zone alone accounts for nearly 50%, whereas the rocky zone, defined as nonmoss above 4 m, produces only 20%, even though it receives the bulk of the light. Spring production (February to the day the snow disappears, about June 15) is highly variable depending on snow cover, but averages only 15% of the annual total production.

The balance between benthic production and respiration and the amount contributed by each meter stratum is shown in Fig. 4. Only the 0–1 m zone is strongly autotrophic, because it is frozen during most of the dark season. The annual compensation depth is about 12–13 m, which also corresponds with the average inner edge of the moss zone (Fig. 1; see **Discussion**). The shallow parts of the lake occupy a larger area and have most of the moss, and therefore contribute much of the lake's respiration, 20% from 0–4 m and 55% from 0–10 m. The shallows are even more important from a photosynthetic viewpoint, with 25% of the production coming from 0–4 m, 53% from 0–7 m, and 90% above 15 m. The average annual photosynthesis per unit area was strongly dependent on depth (Fig. 5), and some years a square meter of moss at 4 m produces over 140 g O_2 m^{-2}.

Discussion

EVALUATION OF THE TECHNIQUE

In general, the use of divers and in situ chambers was satisfactory; however, considerable variation in the data accrued, we think, from the use of the blood–gas analyzer, which required considerable skill for consistent results, and which was dependent on absolute calibration from day to day. We subsequently found, as did Schindler et al. 1973, that using 50-cm^3 samples taken with plastic syringes, fixing the oxygen inside the syringes, and titrating the solution with a microburet gives much higher precision. Then, too, natural variability in the substrate must have effects. The large number of measurements made in this study partially overcame the variability.

More disturbing was a discrepancy between rock respiration rates, about 2 mg m^{-2} h^{-1} in 1971 and 5 mg m^{-2} h^{-1} in 1972. We noted that rounded rocks which had most of their volume below the sediment surface had higher respiration rates when calculated

TABLE 3. Benthic respiration in Char Lake.

Zone	Rate mg O_2 m^{-2} h^{-1}	Annual respiration $\times$ 10^4 g O_2	N	% of bottom area	% total respiration
Sediment	3.77	813.8	56	46.7	35.5
Moss	10.09	1105.8	223	23.9	48.2
Rocky[a]	4.07	375.5	324	29.4	16.3
	Sum	2295.1 $\div 52.6 =$ 43.6 g O_2 m^{-2} yr^{-1}			

[a] Taken as 0–4 m nonmoss.

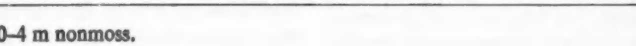


FIG. 4. Depth distribution of benthic photosynthesis and respiration as a percent of the lake total.

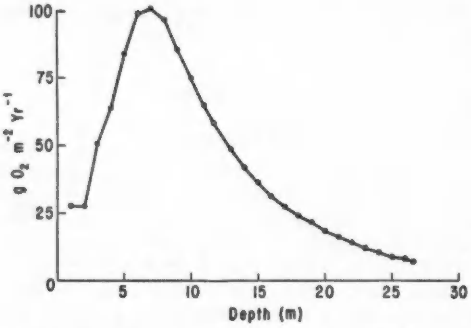


FIG. 5. Average annual benthic photosynthesis in Char Lake.

per area of exposed surface. We thought there might therefore be a positive correlation between respiration rate and surface:volume ratio of the rock, but neither a linear nor second-degree polynomial fit was significant at the 5% level. Nevertheless, the rocks used in 1972 had relatively more subsurface area exposed and might therefore have increased the estimate of respiration rate, but in the absence of further data the mean of the 2 yr was used. Note that the estimate of photosynthesis is unaffected by errors in respiration, as they apply equally to the light chambers.

LIGHT PENETRATION THROUGH SNOW

Our measurement of light transmission through snow was not designed to meet rigorous physical criteria which would enable a complete description of light:snow interactions, but the paucity of data from the arctic snowpack invites fuller discussion of our results. The spring snowpack at Resolute is totally unlike snow further south, due to low snowfall, low temperatures, and high winds. Snow never remains where it falls but drifts many miles, individual grains becoming rounded and dense. The subsequent snow cover is a function of major storms and is composed entirely of drifts of various thickness, the previous storm layers distinct, with the overall texture firm to hard, often resembling balsa wood in surface rigidity. The snow data in Fig. 1 were taken in drifts formed only from one or two storms and the upper 20 cm of snow was uniform in consistency, although grain size increased further down in the snowpack. Our percent transmission over the first few centimeters is similar to that reported by Curl et al. (1972) and Hand and Lundquist (1942), but transmission is about 0.1 that found by Curl et al. at 20 cm for melting alpine snow in Oregon (Fig. 1). Our transmission curve does not follow Lambert's Law, as has been found by recent authors (Curl et al. 1972; Giddings and La Chapelle 1961; Trainor 1947), as the extinction coefficient decreases rapidly with depth; neither does it approximate a straight line when plotted on logarithmic coordinates. Attenuation through the dry arctic snowpack is greater than for other types of snow further south.

The transmission of light through snow and about 2.2 m ice (Fig. 1) appears to be much different than through snow alone; we think this probably results from the broad scattering of light horizontally within the ice column, the result being less light reaching the water below low snow cover, and more below high snow cover than would be expected from snow data alone.

The albedos of about 60–70% (Fig. 1) for the dry snowpack are similar or slightly lower than those determined on fresh or melting snow (Giddings and La Chapelle 1961; Thomas 1965).

In areas where snow cover is variable due to drifting, the use of mean snow cover will underestimate light penetration. Temperate lakes, and even many arctic lakes such as those on the Truelove Lowland, Devon Island (C. K. Minns personal communication) and Lake Hazen on northern Ellesmere Island (Deane 1958) have a uniformly thick snow cover in spring. But lakes in the Resolute area have their entire snow cover in drifted form, often with bare areas alternating with 0.3–0.6 m drifts.

Such drifts are not uniformly distributed over the surface of Char Lake, due to the strong prevailing north winds which erode snow cover on the north side of the lake. Twice in spring 1972 and once in spring 1973, we made a detailed map of snow cover on Char Lake (275 measurements), summarized in Fig. 6. The northern end has less snow cover than the southern end and, in years of low snow cover such as 1968 and 1973, much of the northern side is bare. This could determine the distribution of moss (Fig. 2), which extends to only about 10 m on the south side but down to 19 m on the north side of the lake. Lakes at the same latitude but with higher snow cover than that of Char Lake may not support benthic mosses.

The origin and maintenance of the bare patches within the moss zone was not known, so in spring 1972 we made oxygen measurements on the water lying in these bare depressions and found the oxygen content to be zero, even in patches as small as 0.2 m in diameter. The depressions are 0.2–0.4 m deep and the water within appears turbid or milky all winter and early spring, perhaps due to high anaerobic bacterial populations. Downslope of each depression is a strip of blackened moss, the result of anaero-

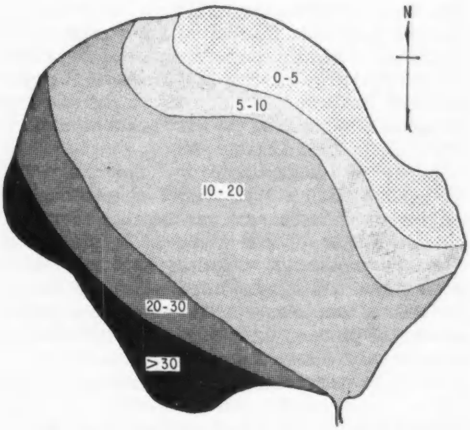


FIG. 6. Snow distribution on Char Lake, spring 1971 and 1972.

bic water slowly spilling from the depression. These depressions could go anaerobic in as little as 1 mo after the onset of the dark season, at a metabolic rate of 0.24 g O_2 m^{-2} day^{-1} in a stable water mass less than 0.5 m thick. We therefore think these patches are maintained on gentle slopes by stagnation of water overwinter. Steep slopes such as are found on the north side of the lake have a few small patches only. We found small holes in the moss, caused by dredging and anchoring, which had become anaerobic and might result in permanent patch formation.

GROSS ENERGY FLOW THROUGH CHAR LAKE

The estimates of annual benthic production (47.5 g O_2 m^{-2}) and respiration (43.6 g O_2 m^{-2}) are close. Planktonic respiration was never detectable and is probably negligible considering the low rate of planktonic production (below). An independent and, we think, more reliable estimate of whole lake respiration derived from winter oxygen curves (Welch 1974) is 40.1 g O_2 m^{-2} yr^{-1}, which again suggests virtually no planktonic respiration when the whole system rate is compared with the benthic estimate alone.

BENTHIC RESPIRATION

The lack of seasonal change in benthic respiration rates, also found by Schindler et al. (1973) for lakes 239 and 240, is noteworthy and corroborates the whole lake respiration rates, which are constant on an exposed bottom area basis from October to April in Char, Resolute, and Water lakes (Welch 1974). Despite year-to-year fluctuations in primary production, there is great stability in overall energy flow, because nearly all the respiration in Char Lake is benthic, and uses as its energy source the detritus present on the bottom. With an oxidized layer 2 cm thick in the deep sediment zone, 90% water and 5% organic material (I. Davies personal communication), there would be 450 kcal m^{-2} in the metabolically active pool, compared with a respiration rate of about 115 kcal m^{-2} yr^{-1}. The detrital pool and cycling of benthic production through this pool stabilizes gross energy flow and probably energy flow at the macroconsumer level as well, as most benthic species in Char Lake are detritivores.

Kalff and Welch (1974) give a mean annual carbon uptake by phytoplankton in Char Lake of 4.2 g C m^{-2} yr^{-1}. Using a conversion factor of 2.75 (Winberg 1971), this gives 11.5 g O_2 which, added to 47.5 g O_2 benthic production, gives a total annual production of 58.0 g O_2 m^{-2} yr^{-1}. Benthic respiration is 43.6 g O_2 m^{-2}, leaving 14.4 g O_2 m^{-2} (25%) difference. Using the whole lake respiration estimate of 40.1 g O_2 m^{-2} yr^{-1} (Welch 1974), 17.9 g O_2 m^{-2} (31%) is the difference. Inflow and outflow of organic matter is probably a minor part of the total energy budget, as suggested by the following: Schindler et al. (1974, table 4) give suspended carbon values averaging 715 mg m^{-3} for inflows 1–4, or 515 mg m^{-3} if one extremely high value for inflow 4 is not used. The outflow average is 398 mg m^{-3}, for a difference of about 0.1 g m^{-3}. Total annual water flow is about 1 m^3 m^{-2} of lake surface, suggesting that net carbon input is at most a few tenths of a gram per square meter. The annual energy storage in Char Lake is therefore about 25–30% of the total energy flow.

Hargrave (1973) has assembled data showing that a mean of 36% of the carbon supply for eight aquatic systems was sedimented; storage would be something less than this. Pamatmat and Bhagwat (1973) have shown that most of the anaerobic metabolism taking place in Lake Washington sediments does not show up on the oxygen budget as measured over intact cores. In Char Lake sediments, with a surface organic content of 5%, anaerobic metabolism is probably much less important than in richer Lake Washington sediment; nevertheless, some portion of the storage is metabolized, with the end products being retained within the sediment and therefore not being included in the respiratory oxygen budget. As benthic invertebrates in Char Lake live within the oxidized layer (unpublished data), their energy flow is probably entirely included in benthic oxidative metabolism with no components coming from the storage term.

Comparative Production Rates

There are no other published arctic studies with data on both benthic and planktonic production. Alexander and Barsdate (1971) found that 11 g C m^{-2} yr^{-1} was fixed in Smith Lake (lat. 65°N, Alaska) by phytoplankton and suggested that as much again might be fixed by phytobenthos. As Smith Lake is only 3.5 m maximum depth, however, benthic photosynthesis is probably much higher. Comita and Edmondson (1953) reported an average of 0.75 g C m^{-2} day^{-1} for phytoplankton photosynthesis in shallow (2.7 m $\bar{z}_m$) Imikpuk Lake, Barrow, Alaska. Goldman (1960) estimated the carbon fixation of deep (78 m $\bar{z}_m$) Brooks Lake, lat. 58°N, Alaska, at 35–40 g C m^{-2} yr^{-1}. Howard and Prescott (1971) reported volume-based summer carbon uptake rates for Alaskan North Slope and shallow coastal lakes averaging 15–220 mg C m^{-3} day^{-1}. On the basis of phytoplankton production alone, therefore, Char Lake is much less productive than these more southerly Alaskan lakes.

Four studies, summarized in Table 4, are of particular interest from a comparative point of view, because they deal with both benthic and planktonic photosynthesis. As might be expected, shallow lakes like Borax and Marion have most of their autotrophic production centered in the benthos. Even deeper lakes like Char and Lawrence are dominated by benthic photosynthesis when the benthic autotrophic community presents a thick chlorophyll layer (mosses, macrophytes, etc.). Lakes 239 and 240 differ sharply in that benthic photosynthesis is negligible compared with that of the phytoplankton. There are almost no macrophytes in these two lakes, the effective depth of photosynthesis is only about 5 m due partly to the brown color of the water, and there is a flocculent muck bottom below 5 m. The benthic oxygen data given by Schindler et al. was 4 times higher than the CO_2 data used, and their phytoplankton carbon figures include about a threefold filtration correction factor (Arthur and Rigler 1937; Schindler and Holmgren 1971) which was not used in the other C^{14} phytoplankton studies. Even if valid, however, these changes would increase the benthic contribution to only 15% in lakes 239 and 240.

Table 4 also demonstrates the extreme oligotrophic nature of Char Lake; many lakes throughout the world metabolize more per day than Char does annually (Brylinsky and Mann 1973; Eley 1970). This low production rate does not result solely from a low light input. Variation in methods and the lack of complete seasonal studies make comparison of photosynthetic efficiencies difficult, but several points emerge.

First, the response of the phytobenthos to light was of two types. The rocky zone photosynthetic rate was independent of light and therefore exhibited a variable, usually low, efficiency. For example, the average radiation at 1-m in August is about 35 kcal m^{-2} h^{-1}, and the average photosynthetic rate is 10.44 mg O_2 or 36.5 kcal m^{-2} h^{-1}, for an efficiency of 0.1%. Schindler et al. (1973) also found no correlation between light and carbon uptake in preliminary experiments on epilithic algae in lakes 239 and 240. However, Char Lake moss and sediment zones responded linearly up to about 150 kcal m^{-2} h^{-1} light, at an efficiency of 1.0%. In comparison, Hargrave (1969) found efficiencies of 0.4–3.1% for phytobenthos in Marion Lake, and reported no evidence of photoinhibition at light levels as high as 450 kcal m^{-2} h^{-1}. Benthic photosynthesis in Lawrence and Borax lakes must also have been more efficient than in Char Lake.

Secondly, the lake as a whole is less efficient in its use of light than southern lakes, due in part to photoinhibition of phytoplankton photosynthesis at moderate to high light levels (Kalff and Welch 1974). Surface radiation is 4×10^5 kcal m^{-2} yr^{-1}

TABLE 4. Annual benthic and plankton photosynthesis in freshwater lakes.

Author	Lake	Area (*ha*)	$\bar{z}$,m	Total g C m^{-2} yr^{-1}	Percent benthic
Wetzel 1964	Borax	39.8	<.5	404.9	75
Hargrave 1969 Efford 1970 Davies 1970	Marion	13.3	2.2	66.0	88
Wetzel et al. 1972	Lawrence	5.0	5.9	171.1	75
Schindler et al. 1973	239	56.1	10.5	83.1	1
	240	44.1	6.1	51.0	2
this study	Char	52.6	10.2	21.1	80

with production of 290 kcal m^{-2} yr^{-1}, for an efficiency of 0.07%. An average of 0.95×10^5 kcal m^{-2} yr^{-1} enters the water, for an efficiency of 0.3%. These are much lower than for Clear Lake (Schindler and Nighswander 1970) and for the lakes discussed by Brylinsky and Mann (1973), even considering phytoplankton alone. Brylinsky and Mann found that variables related to solar energy had a greater influence on production than variables related to nutrient concentration; however, latitude and air temperature explained over 50% of the variance on a global basis, whereas visible radiation explained less than 1%. Their figure 10C, relating photosynthetic efficiency with phytoplankton production, suggests there was a small range in radiation and a large range in phytoplankton production, resulting in a nearly constant rate of change in photosynthetic efficiency as production increased.

The reasons for the relatively low overall efficiency of light utilization in Char Lake may lie in the very low nutrient loading (Schindler et al. 1974). The low response of the shallow phytobenthos to light, as compared with littoral macrophytes further south, also contributes to the low overall efficiency. As most respiration is benthic, the nutrients recycled during heterotrophic activity, coupled with the thicker chlorophyll layer, may be the reasons for the much higher efficiencies of deeper phytobenthos compared with phytoplankton in Char Lake.

Acknowledgments

This work was facilitated by numerous people. Special thanks go to A. Caron, G. Kearsly, J. Burgener, and A. Atagotaluk for their diving skills. A. Sreedharan, B. Shuter, and R. Buie helped with data analysis. H. Harvey, F. Rigler, and D. Schindler provided useful comments on the manuscript.

Alexander, V., and R. J. Barsdate. 1971. Physical limnology, chemistry and plant productivity of a taiga lake. Int. Rev. Ges. Hydrobiol. 56: 825–872.

Arthur, C. R., and F. H. Rigler. 1967. A possible source of error in the C^{14} method of measuring primary productivity. Limnol. Oceanogr. 12: 121–124.

Brylinsky, M., and K. H. Mann. 1973. An analysis of factors governing productivity in lakes and reservoirs. Limnol. Oceanogr. 18: 1–14.

Carpenter, J. H. 1965. The Chesapeake Bay Institute technique for the Winkler dissolved oxygen method. Limnol. Oceanogr. 10: 141–143.

Comita, G. W., and W. T. Edmondson. 1953. Some aspects of the limnology of an Arctic lake. Stanford Univ. Publ. Biol. Ser. XI: 7–13.

Curl, H. Jr., J. T. Hardy, and R. Ellesmeier. 1972. Spectral absorption of solar radiation in alpine snowfields. Ecology 53: 1189–1194.

Davies, G. S. 1970. Productivity of macrophytes in Marion Lake, British Columbia. J. Fish. Res. Board Can. 27: 71–81.

Deane, R. E. 1958. Pleistocene geology and limnology, p. 19–23. *In* "Operation Hazen," narrative and preliminary reports for the 1957 season, preliminary scientific reports, geology. Def. Res. Board, Ottawa, Rep. D. Phys. R (G) Hazen 2.

Efford, I. E. 1967. Temporal and spatial differences in phytoplankton productivity in Marine Lake, British Columbia. J. Fish. Res. Board Can. 24: 2283–2307.

Eley, R. L. 1970. Physicochemical limnology and community metabolism of Keystone Reservoir, Oklahoma. Ph.D. Thesis. Oklahoma State Univ., Stillwater, Okla. 239 p.

Giddings, J. C., and E. La Chapelle. 1961. Diffusion theory applied to radiant energy distribution and albedo of snow. J. Geophys. Res. 66: 181–189.

Goldman, C. R. 1960. Primary productivity and limiting factors in three lakes of the Alaska peninsula. Ecol. Monogr. 30: 207–230.

Hand, I. F., and R. E. Lundquist. 1942. Observations of radiant penetration through snow. Mon. Weather Rev. 70: 22–25.

Hargrave, B. T. 1969. Epibenthic algal production and community respiration in the sediments of Marion Lake. J. Fish. Res. Board Can. 26: 2003–2026.

Howard, H. H., and G. W. Prescott. 1971. Primary production in Alaskan tundra lakes. Am. Midl. Nat. 85: 108–123.

Kalff, J., and H. E. Welch. 1974. Phytoplankton photosynthesis in Char and Meretta lakes, Cornwallis Island. J. Fish. Res. Board Can. 31: (This issue).

Pamatmat, M. M., and A. M. Bhagwat. 1973. Anaerobic metabolism in Lake Washington sediments. Limnol. Oceanogr. 18: 611–627.

Rigler, F. H. 1970. The Char Lake Project: A study of energy flow in a high Arctic lake, p. 287–300. *In* Z. Kajak and A. Hillbricht-Ilkowska [ed.] Productivity problems of freshwaters. Warszawa and Krakow.

Ruttner, F. 1963. Fundamentals of limnology. Univ. Toronto Press, Toronto, Ont. 295 p.

Schindler, D. W., V. E. Frost, and R. V. Schmidt. 1973. Production of epilithiphyton in two lakes of the Experimental lakes area, northwestern Ontario. J. Fish. Res. Board Can. 30: 1511–1524.

Schindler, D. W., and S. K. Holmgren. 1971. Primary production and phytoplankton in the Experimental Lakes area, northwestern Ontario, and other low-carbonate waters, and a liquid scintillation method for determining ^{14}C activity in photosynthesis. J. Fish. Res. Board Can. 28: 189–201.

Schindler, D. W., and J. E. Nighswander. 1970. Nutrient supply and primary production in Clear

Lake, eastern Ontario. J. Fish. Res. Board Can. 27: 2009–2036.

Schindler, D. W., H. E. Welch, J. Kalff, G. J. Brunskill, and N. Kritsch. 1974. Physical and chemical limnology of Char Lake, Cornwallis Island (75° N lat.). J. Fish. Res. Board Can. 31: 585–607.

Thomas, C. W. 1965. On the transfer of visible radiation through sea ice and snow. J. Glaciol. 4: 481–484.

Trainor, L. 1947. The spectral reflection and absorption of radiation by snow. M.A. Thesis. Univ. Saskatchewan, Saskatoon, Sask.

Welch, H. E. 1974. Metabolic rates of high Arctic lakes. Limnol. Oceanogr. (In press)

Wetzel, R. G., P. H. Rich, M. C. Miller, and H. L. Allen. 1972. Metabolism of dissolved and particulate detrital carbon in a temperate hard-water lake. Mem. Ist. Ital. Idrobiol. (Suppl.) 29: 815–244.

Winberg, G. G. [ed.] 1971. Symbols, units and conversion factors in studies of freshwater productivity. IBP (PF) Pam. IBP Central Office, London.

Phytoplankton Production in Char Lake, a Natural Polar Lake, and in Meretta Lake, a Polluted Polar Lake, Cornwallis Island, Northwest Territories[1,2]

J. KALFF

Department of Biology, McGill University, Montreal, Que.

AND H. E. WELCH[3]

Department of Zoology, University of Toronto, Toronto, Ont.

KALFF, J., AND H. E. WELCH. 1974. Phytoplankton production in Char Lake, a natural polar lake, and in Meretta Lake, a polluted polar lake, Cornwallis Island, Northwest Territories. J. Fish. Res. Board Can. 31: 621–636.

Phytoplankton production of ultraoligotrophic Char Lake and polluted Meretta Lake (lat. 74° 42′ N; long. 94° 50′W) were studied between 1969 and 1972. Phytoplankton production in Char Lake is approximately 4.1 g C m^{-2} yr^{-1}, making it the most oligotrophic lake on record. Photosynthesis takes place virtually the whole 9 mo the sun comes above the horizon. Changes in depth of maximum photosynthesis, in efficiency of low light utilization, and in optimal light flux resulted in a much more constant production rate than suggested by the light input, which is importantly affected by amount of snow cover. Phytoplankton in nearby sewage-polluted Meretta Lake averages 11.3 g C m^{-2} yr^{-1}, and chlorophyll concentrations are 20 times higher than in Char Lake. Nutrient deficiencies, especially of phosphorus, are almost certainly responsible for the low efficiency of light utilization and resulting low production in Char Lake. Benthic production is of major significance in both lakes.

KALFF, J., AND H. E. WELCH. 1974. Phytoplankton production in Char Lake, a natural polar lake, and in Meretta Lake, a polluted polar lake, Cornwallis Island, Northwest Territories. J. Fish. Res. Board Can. 31: 621–636.

Nous avons étudié la production de phytoplancton dans le lac ultra-oligotrophe Char et le lac pollué Meretta (lat. 74°42′N; long. 94°50′W) de 1969 à 1972. La production de phytoplancton dans le lac Char est approximativement de 4.1 g C m^{-2} an^{-1}, ce qui fait de lui le lac le plus oligotrophe jamais enregistré. Il y a photosynthèse pratiquement durant les 9 mois où le soleil se montre au-dessus de l'horizon. Les changements de profondeur de photosynthèse maximale, de l'efficacité d'utilisation d'une faible intensité lumineuse et de l'influx lumineux maximal résultent en un taux de production beaucoup plus constant que ne le suggère l'apport de lumière, lui-même fortement affecté par l'épaisseur de la couche de neige. La production de phytoplancton dans le lac Meretta avoisinant et fortement pollué par les égouts est de 11.3 g C m^{-2} an^{-1} en moyenne, et les concentrations de chlorophylle sont 20 fois plus élevées que dans le lac Char. Des déficiences en substances nutritives sont presque certainement responsables de la faible efficacité de l'utilisation de la lumière et de la faible production qui en résulte dans le lac Char. La production benthique a une importance majeure dans les deux lacs.

Accepted January 31, 1974

---

[1] This paper, part of a special issue that comprises a comprehensive review of Limnology in Canada, was prepared to mark the 19th Congress of the International Association of Limnology (SIL), in Winnipeg, Man., during August 1974.

[2] Contribution no. 255 of the Canadian Committee for IBP and contribution no. 23 of the Char Lake Project.

[3] Present address: Department of the Environment, Fisheries and Marine Service, St. Andrews, N.B.

Printed in Canada (J3298)

MOST conditions encountered by phytoplankton in polar lakes are not unique when considered individually. Low temperatures are also experienced by phytoplankton in temperate lakes during winter, and prolonged snow cover on these lakes simulates the near darkness of the polar winter. Tropical and temperate lakes occurring in granitic regions sometimes have low nutrient levels similar to those in polar lakes. Nevertheless, polar phytoplankton live at one extreme of a spectrum of tolerable environmental conditions, and experience continuous cold, extremely low nutrient concentrations, and an extended period of near-darkness. Yet they appear to have no peculiar adaptations to these conditions, as their production rates are unusually low (Kalff 1970; Hobbie 1973). Consequently, study of algae living under these extreme conditions, on which a dramatic annual cycle in daily photosynthetically active energy flux is superimposed, might reveal something new about the control of phytoplankton production and abundance.

Our purpose was to study phytoplankton populations and production in an ultraoligotrophic polar lake over several years and compare it with a nearby sewage-enriched lake (Kalff et al. 1972; Schindler et al. 1974a). In this paper we present the results of ^{14}C fixation measurements in Char Lake over 3½ yr, and compare them with phytoplankton biomass (chlorophyll *a*) and with production in enriched Meretta Lake. The setting and physical-chemical limnology of Char Lake were described by Rigler (1972) and Schindler et al. (1974a). Meretta Lake is described by Schindler et al. (1974a) and pigment cycles in both lakes are described by Kalff et al. (1972).

Methods

Samples for the measurement of phytoplankton production (^{14}C) were collected at weekly intervals between May and September 1969 and 1970, and biweekly during the same periods in 1971 and 1972. Approximately biweekly sampling was done during the remainder of the 3½ yr. Samples were collected with an opaque van Dorn bottle at 2, 3, 5, 7.5, 10, 15, 20, and 25 m and poured into calibrated light and dark bottles with a capacity of approximately 132 ml each. Samples were taken from 0 and 1 m when ice thickness allowed. To each bottle was added 1.0 ml, and during the early growing season sometimes 2.0 ml, of $Na^{14}CO_3$ with an absolute activity of different batches varying from 25 to 28 μg/ml as determined by van Slyke combustion and gas-phase assay. The samples were resuspended at the depth of collection and incubated for 4–5 h between approximately 1100 and 1500–1600. Occasionally 6-h incubations were made throughout 24 consecutive hours. Care was taken to prevent light shocking the algae during the manipulations, which were carried out over the hole in a darkened hut, under blankets, or in a darkened snow-vehicle adjacent to the hole. The whole content of each bottle was normally filtered through 0.45-μ membrane filters approximately ½ h after collection. Chlorophyll *a* (hereafter referred to as chlorophyll) was determined by fluorometry of material extracted by 90% acetone without grinding (Kalff et al. 1972). Surface radiation was measured daily and in situ light measured at time of sampling. Instrumentation and method of calculating the light received at each meter depth is described in Schindler et al. (1974b) and Welch and Kalff (1974). Our methods for estimating annual phytoplankton photosynthesis are described in the next section. Symbols are defined in Appendix 1.

Results

CALCULATION OF TOTAL PHYTOPLANKTON PRODUCTION

Our first approach was to multiply production times lake volume at each depth to obtain production per m^2 of lake surface for each of the 68 incubation periods, and then expand to a 24-h production rate by multiplying by the ratio (light received during 24 h)/(light received during the incubation period), assuming a linear relation between light and photosynthesis throughout the day. The mean monthly production rates using this technique are shown in Fig. 1 and Table 1, column A; the average annual carbon fixation by this method is 2.8 g m^{-2} yr^{-1} in Char Lake.

We then examined the correlation of carbon uptake and carbon uptake per unit chlorophyll, with light at different light intensities (Table 2). In both Char and Meretta lakes, there is a rapid decrease in slope as higher light levels are included in the analysis, suggesting a curvilinear relation between light and carbon uptake. As expected, the level of carbon uptake per unit light in Meretta is about 20 times higher than in Char. However, there is no significant difference between the two lakes in terms of milligrams carbon uptake per milligram chlorophyll.

An attempt to fit a polynomial to the carbon: light data was unsuccessful because the response at higher light levels was extremely variable and appeared to change with time. A plot of I_{opt} (Fig. 2), the light level at which maximum photosynthesis per unit chlorophyll occurs, confirmed that phytoplankton populations were responding differently to the same light levels as summer progressed, generally becoming adapted to higher light in July–August. We then combined the data for all the years by month and plotted the mean carbon uptake at 5 kcal m^{-2} h^{-1} intervals if there were four or more values within an interval, and fitted curves by eye to the data for each month. The results (Fig. 3 and 4) show clearly that in Char, the photosynthetic response at high levels increases from June to August, then decreases in September. Light levels (20 kcal m^{-2} h^{-1}) that are inhibitory in July are not inhibitory in August. In Meretta, photosynthesis is highest at high light in July and decreases in August.

Lastly we plotted mg C m^{-3} h^{-1} against light for each month within the 0–5 kcal m^{-2} h^{-1} range and fitted straight lines by eye through the origin; the results are in Table 3. Figure 3 and 4 and Table 3 are our best description of seasonal changes in carbon uptake at different light intensities.

To obtain a better estimate of annual photosynthesis in Char Lake than those given above, we divided total monthly irradiance at each meter depth by hours in each month, applied these hourly radiation rates against the results in Fig. 3 and Table 3, and computed a mean photosynthesis for 1970–72 of 5.2 g C m^{-2} yr^{-1} (Table 1, column B). This errs on the high side, however, because irradiance varies diurnally, and taking a mean hourly rate over 24 h and applying this against a strongly curvilinear photosynthetic response (Fig. 3) overestimates daily production. Therefore, we divided the mean daily radiation at each meter depth for each month into six 4-h units, based on the average surface irradiance received within each 4-h period

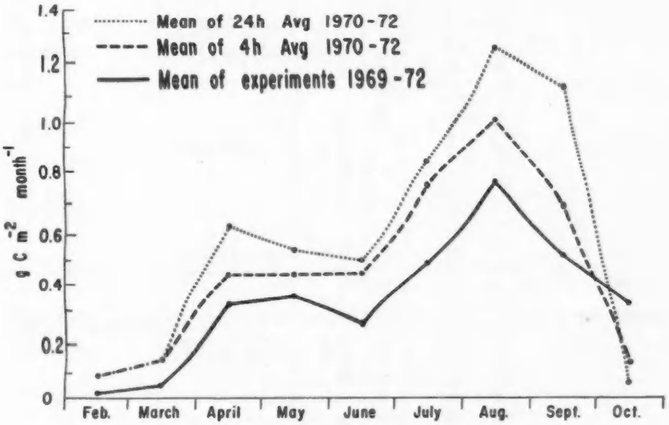


FIG. 1. Mean annual carbon uptake in Char Lake.

TABLE 1. Photosynthesis (g C m^{-2} $month^{-1}$) in Char Lake.

	A	B	C	D	E	F
	Mean 1969–72 experiments	Mean 1970–72 24-h avg	Mean 1970–72 4-h avg	1970 4-h avg	1971 4-h avg	1972 4-h avg
Feb.	.036	.098	.098	.070	.179	.044
Mar.	.041	.153	.153	.209	.202	.048
Apr.	.210	.629	.443	.530	.494	.304
May	.288	.539	.445	.552	.553	.229
June	.205	.502	.447	.439	.509	.394
July	.411	.843	.755	.751	.722	.793
Aug.	.744	1.248	1.017	.952	1.098	1.000
Sept.	.539	1.125	.689	.655	.718	.695
Oct.	.320	.062	.139	.110	.257	.050
Sum, g C m^{-2} yr^{-1}	2.794	5.199	4.186	4.268	4.732	3.557
% difference from column C	−33%	+24%	0.0%	+2%	+13%	−15%

TABLE 2. Correlations between light (kcal m^{-2} m^{-1}) and photosynthesis (mg C m^{-3} h^{-1}; mg C m^{-3} mg Chl^{-1}) in Char Lake, 1969–71. $Y_{1,2} = A + BX$. X = kcal m^{-2} h^{-1}, Y_1 = mg C m^{-3} h^{-1}, Y_2 = mg C Chl^{-1}.

	Char						Meretta					
	mg C m^{-3} h^{-1}			mg C m^{-3} mg Chl^{-1}			mg C m^{-3} h^{-1}			mg C m^{-3} mg Chl^{-1}		
Light (kcal m^{-2} h^{-1})	Correlation (*r*)	Slope (B)	Number (N)	Correlation (*r*)	Slope (B)	Number (N)	Correlation (*r*)	Slope (B)	Number (N)	Correlation (*r*)	Slope (B)	Number (N)
≤2.5	.43	.14	117	.55	.46	108	.37	2.59	52	.38	.43	51
≤5.0	.52	.11	155	.68	.35	143	.62	2.87	65	.53	.37	63
≤10.0	.54	.08	174	.69	.27	162	.59	1.76	77	.56	.29	75
≤15.0	.51	.05	186	.68	.22	174	.57	1.18	86	.65	.27	84
All data	.48	.01	273	.52	.04	260	.39	.23	124	.59	.10	122

for each month, and recalculated production using these rates plus Fig. 3 and Table 3. The result (Table 1, columns C–F), giving a mean of 4.2 g C m^{-2} yr^{-1}, is our best estimate of phytoplankton photosynthesis in Char Lake. We then used the same procedure for Meretta Lake, for the period June 15–September 30 only. We have no comprehensive snow cover measurements for Meretta, and therefore no subsurface spring light data, but the spring snow cover in 1969–72 was much higher on Meretta than Char, averaging about 20 cm with no bare ice surface; so, based on our short-term midday incubation, the total production before June 15 and after September is less than 10% of the total. Mean annual phytoplankton photosynthesis in Meretta is therefore about 11.3 g C m^{-2} yr^{-1} (Table .4)

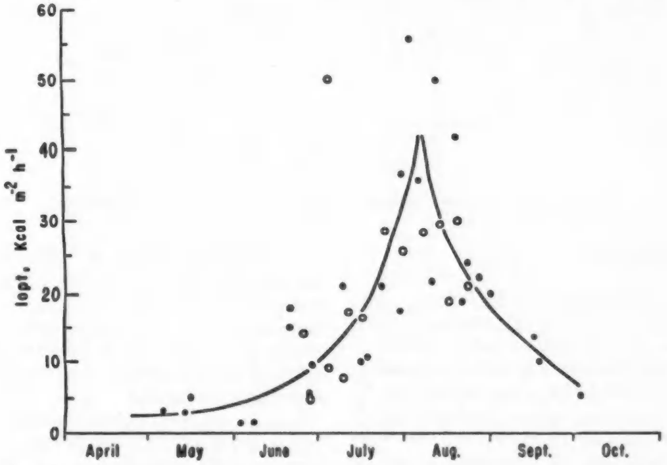


FIG. 2. I_{opt} in Char and Meretta lakes, 1969–72. M Char Lake; M Meretta Lake.

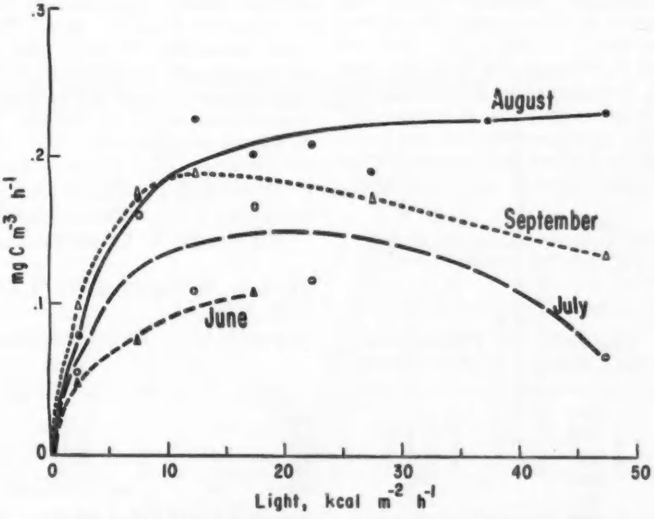


FIG. 3. Primary production vs. light by month, Char Lake.

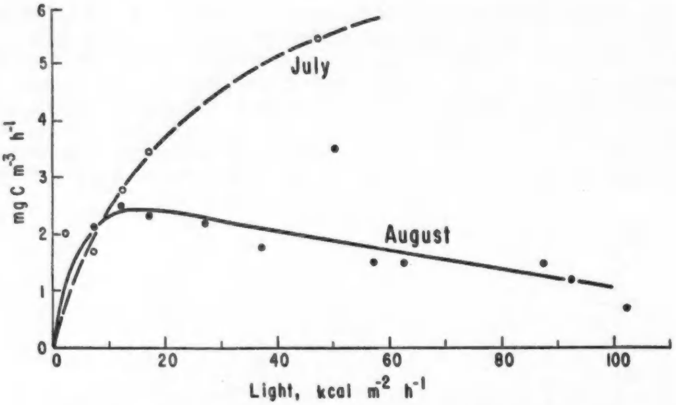


FIG. 4. Primary production vs. light by month, Meretta Lake.

PATTERNS OF PRODUCTION

Phytoplankton production in Char Lake commenced in the surface water shortly after the return of the sun above the horizon in early February, and the photic zone gradually deepened as increasing radiation reached the lake (for example, see Fig. 5). Production rates rose from approximately 4 mg C m^{-2} day^{-1} in February to 15 mg C m^{-2} day^{-1} in April, May, and June (Fig. 1). The constant rate of production from April to early June is the result of interaction between increasing snow cover, increasing surface light (Schindler et al. 1974b), and decreasing photosynthetic efficiency (Table 3). Following the onset of the spring melt in mid-June, average daily rates rise to 32 mg C m^{-2} day^{-1} in August (Fig. 1 and 5), although the increase is not nearly as great as the increase in subsurface light levels (Schindler et al. 1974b, Fig. 5). Production rapidly declines after development of a snow cover in late September and terminates shortly before the onset of the polar night in early November, after a growing season of 9 mo. About 20% of the annual phytoplankton production takes place under winter conditions between February and mid-June (similar to the 15% spring benthic production reported by Welch and Kalff 1974) and a negligible quantity under the equivalent conditions in October and early November.

Based on incubation experiments performed under average snow conditions (not the same as average light conditions — see Welch and Kalff 1974), the photic zone reaches the maximum depth (27 m) about mid-April. However, the midday depth of maximum photosynthesis ($n\mathrm{P}_{\max}$) remains in the surface waters approximately until the photic zone reaches maximum depth (Fig. 6). The $n\mathrm{P}_{\max}$ starts descending in April, reaches 25 m by mid-June, and remains associated with light intensities ($n\mathrm{I}_{\mathrm{opt}}$) of 50 kcal m^{-2} day^{-1} or less. The $n\mathrm{P}_{\max}$ then begins ascending and reaches the lake surface in August, remaining at or near the surface through the remainder of the growing season (Fig. 6). The ascending limb of $n\mathrm{P}_{\max}$ is associated with rapidly rising $n\mathrm{I}_{\mathrm{opt}}$ values which reach 600 kcal m^{-2} day^{-1} in July–August. In September $n\mathrm{I}_{\mathrm{opt}}$ rapidly returns

TABLE 3. Relation between primary production (mg C m^{-3} h^{-1}) and light (kcal m^{-2} h^{-1}) in Char and Meretta lakes, 1969–71.

	Char Lake (*mg C kcal*$^{-1}$)	Meretta Lake (*mg C kcal*$^{-1}$)
Feb.–April	.066	–
May	.048	–
June	.032	.16
July	.026	.40
Aug.	.032	.40
Sept.–Oct.	.044	.16

TABLE 4. Production (g C m^{-2} $month^{-1}$) in Meretta Lake, 1970–72.

	1970	1971	1972
June	.62	.92	.49
July	5.16	5.21	4.52
Aug.	3.93	3.91	2.89
Sept.	2.16	2.51	1.47
Annual, g C m^{-2} yr^{-1}	11.9	12.5	9.4

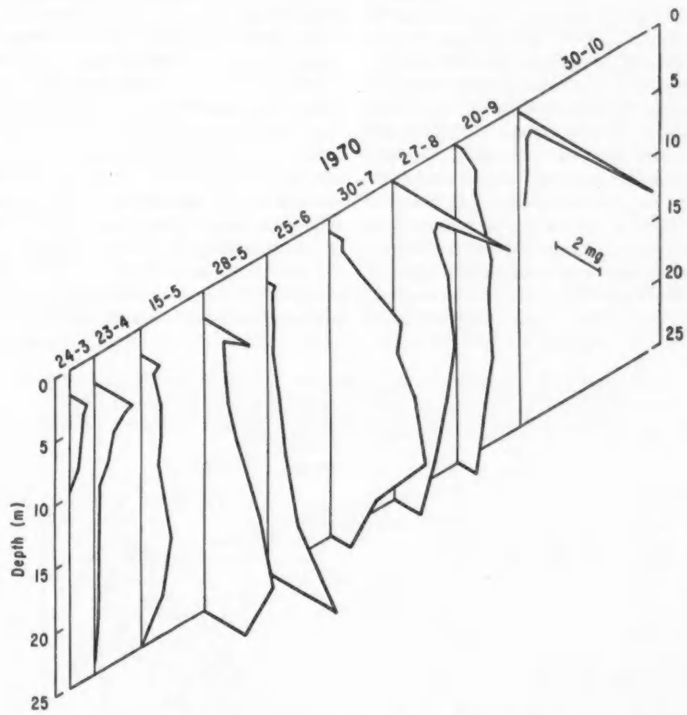


FIG. 5. Vertical production patterns (mg C m^{-3} day^{-1}) in Char Lake, 1970.

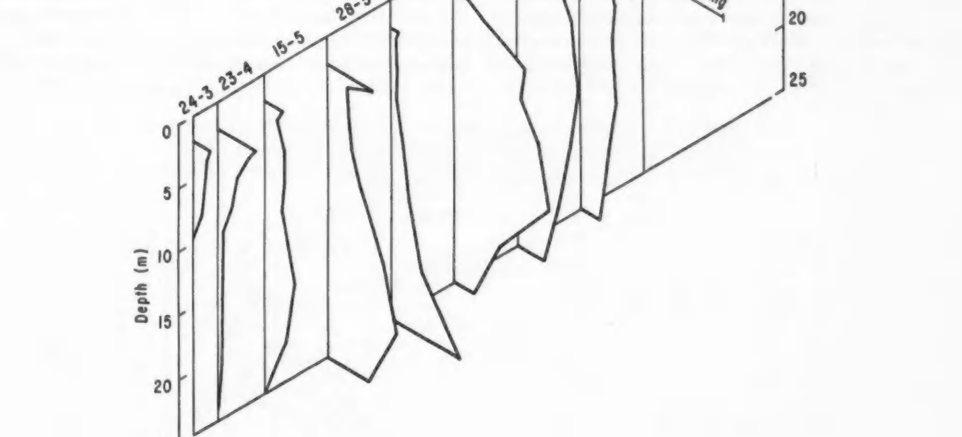


FIG. 6. Depth of maximum production ($n\mathrm{P}_{\mathrm{max}}$) during midday incubations in 1970. Black and clear areas on the histograms show approximate lower and upper limits of light associated with the $n\mathrm{P}_{\mathrm{max}}$.

to the low spring levels. The maximum photosynthetic rate per unit of chlorophyll (P_{max}) parallels nP_{max} prior to June, indicating that nP_{max} was the result of relatively high photosynthetic activity per unit chlorophyll rather than a shift in biomass.

The diurnal pattern of photosynthesis was determined on July 9 and 10 1970, when 3750 kcal m^{-2} surface radiation was received over the 24 h used (Fig. 7). The midday incubation gave the largest photosynthesis in deep water but this was counteracted by photoinhibition at the surface. The depth of nP_{max} changed with changing light intensities, but nP_{max} remained at approximately 90 μg C m^{-3} h^{-1} during the 24 h. The phytoplankton down to 15 m appears to have been equally light-adapted because nP_{max} remained associated with a constant mean light flux of 10–20 kcal m^{-2} h^{-1}. Diurnal movements of phytoplankton were not likely responsible for the large changes in the depth of nP_{max}.

On two occasions we checked for diurnal vertical migration; one test, in August 1972 when the lake was largely ice-covered, was done at 1-m intervals every 4–6 h. The results (Fig. 8) at first suggest no marked diurnal changes in chlorophyll but as there was no marked stratification of chlorophyll, vertical migration could have taken place without changing the chlorophyll concentrations at mid depth. Although mean chlorophyll m^{-3} does not change significantly during the day, the mean chlorophyll concentration of 1 and 2 m com-

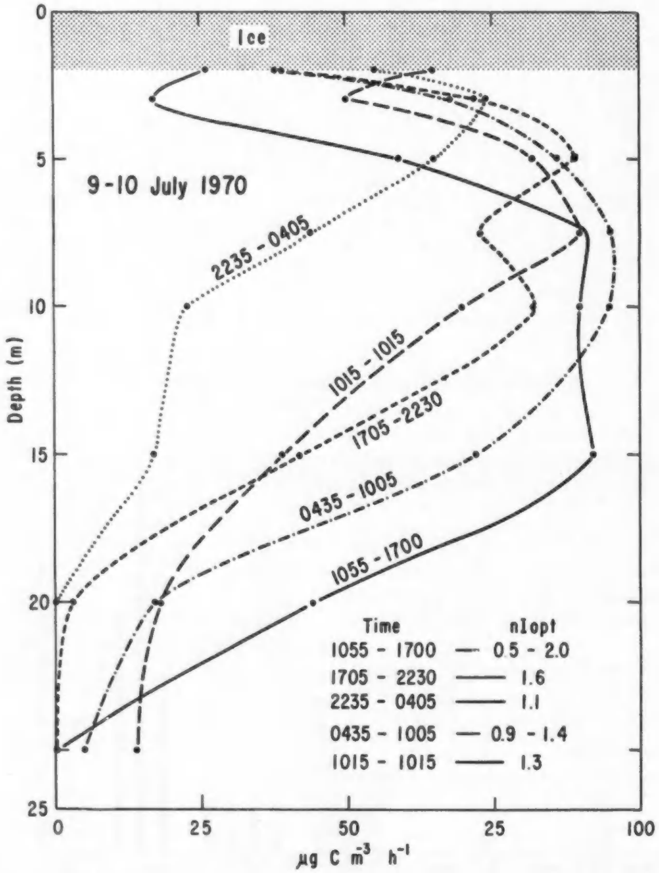


FIG. 7. Diurnal vertical production in Char Lake, July 9–10, 1970 showing the nI_{opt} associated with nP_{max} and nI_{opt} as kcal m^{-2} h^{-1} × 10^1.

bined does increase sharply at night and decreases during the day (Fig. 9). Furthermore, the depth of the chlorophyll center of gravity shifts 3–4 m diurnally, rising at night and falling during the day. The distance of this vertical migration is similar to the 2.5–7.5 (mean 4.2) m diurnal shift found by Tilzer (1973) in a temperate zone alpine lake.

The annual chlorophyll cycle differs between the two lakes. Char Lake has a build-up beneath the ice in spring, a rapid decrease just before melt, and a lower secondary peak in August (Fig. 10). Note that the spring increase is delayed in years of high snow cover (1971, 1972). Meretta has a slower increase in spring chlorophyll almost certainly due to the thicker snow cover and resulting decreased light levels and has a single sharp peak in chlorophyll occurring just after the heavy runoff of melted sewage (Fig. 11).

To examine vertical and seasonal changes in photosynthetic characteristics of the phytoplankton, samples were collected and resuspended both at the depth of collection and at other depths in May, June, July, and August. The results (Fig. 12–15) show a surprising identity in the I_{opt} of samples from all depths on a given sampling date, despite the cells having presumably been grown at different light intensities. The I_{opt} gradually increased from 3 kcal m^{-2} h^{-1} (or more) in May to 20 kcal m^{-2} h^{-1} during the open-water period in August, at the same time that the efficiency of low light utilization also declined (Table 2 and 3). These are not temperature effects because the water temperature

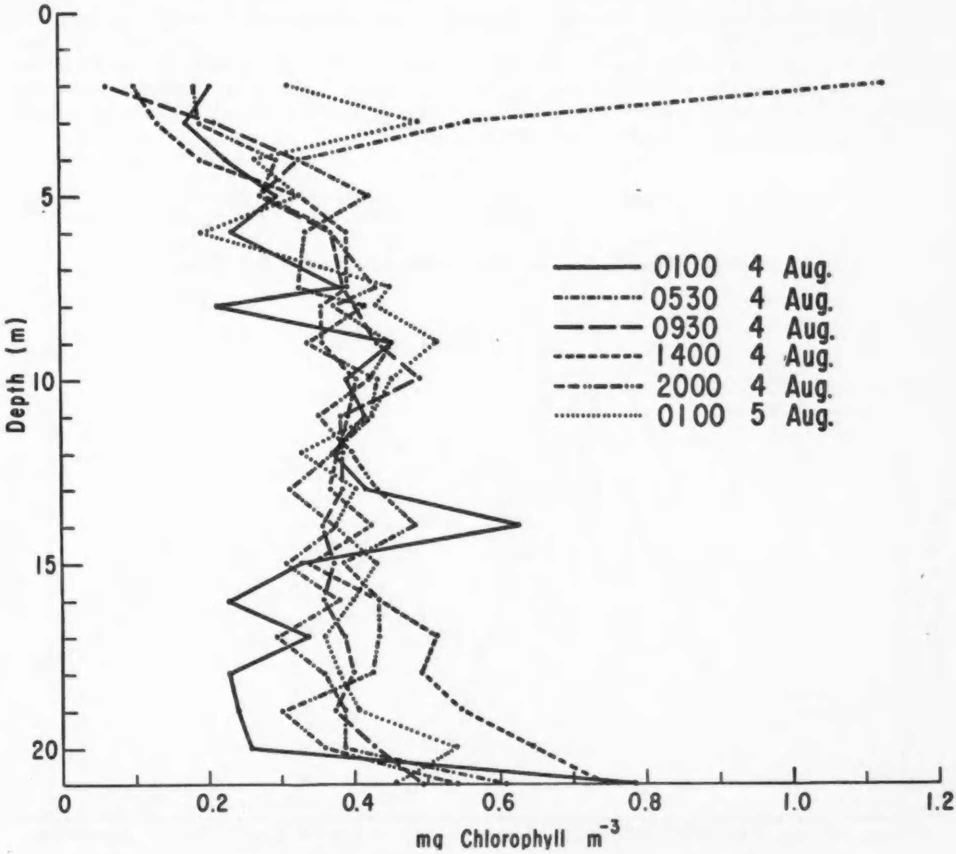


FIG. 8. Chlorophyll a, mg m^{-3} vs. depth in Char Lake, August 4–5, 1972.

changes very little (Schindler et al. 1974b). Light inhibition in the 2 and 5-m samples in June and July and August is probably largely responsible for the lowered lake photosynthetic efficiency during these months (Table 3).

The photosynthetic activities of the 15-m samples in May and June and of the 20- and 25-m samples in July (Fig. 12–14) were relatively high. The ability of phytoplankton from these depths to increase their photosynthesis substantially when exposed to more optimal light suggests a better nutrient environment here than higher up in the water column. The depth of maximum photosynthetic potential in May, June, and early July coincides with the depth at which nP_{max} was then found (Fig. 6), indicating that the nP_{max} found in deep

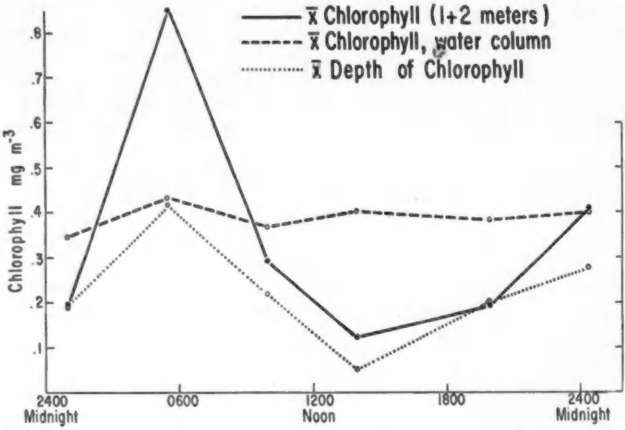


FIG. 9. Chlorophyll a, mg m^{-3} in Char Lake, August 4–5 1972.

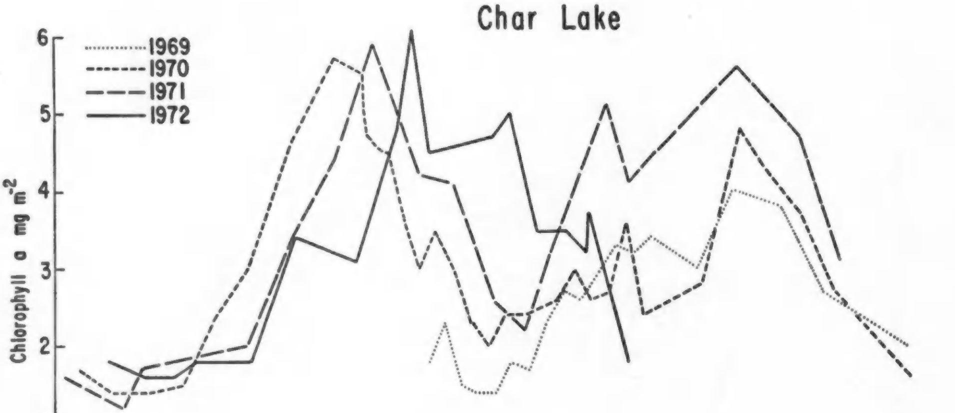


FIG. 10. Chlorophyll a, mg m^{-2} for 1969–72 in Char Lake.

water in May-June is a result of both a more suitable light climate and nutrient environment than higher in the water column.

Discussion

The phytoplankton production rates presented were not corrected for a possible loss of organic matter during filtration. The need for this was suggested by Authur and Rigler (1967) and further elaborated by Schindler et al. (1972). A series of experiments at Char and Meretta lakes indicated that if such a correction is indeed necessary, the results presented for the two lakes should be increased approximately five- and threefold, respectively. However, recent work by Nalewajko and Lean (1972) and McMahon (1973) questions the validity of the so-called correction factors in ^{14}C production studies, while Rudd and Hamilton (1973), using an ATP assay, demonstrated that it is unlikely that cell breakage upon filtration is responsible for the "filtration error." With the present contradictory evidence we did not consider the application of correction factors to our data warranted.

The production rates presented here are based on incubations carried out during the late morning–early afternoon period. This covers only a quarter of the light period when the sun remains above the horizon for 24 h. On 10 days in June–August, we investigated the diurnal pattern of photosynthesis by running a series of incubations of 5–6 h duration, plus a 24-h incubation over the same time period. We found (as did Tilzer 1973) no diurnal change in photosynthetic efficiency for individual bottles. The area-based sum of the short-time incubations was also not significantly different from the 24-h incubation (Fig. 16), indicating absence of the bottle effects sometimes associated with long incubations in the temperate zone.

The diurnal constancy of $n\mathrm{I}_{\mathrm{opt}}$ on July 9 and 10 was matched seasonally by a $n\mathrm{I}_{\mathrm{opt}}$ which changed little between late April and early July (Fig. 6). By moving away from the surface the $n\mathrm{P}_{\mathrm{max}}$ remained associated with approximately the same flux as in the surface waters in April. Once the lake bottom was reached and light levels kept increasing the $n\mathrm{I}_{\mathrm{opt}}$ rose, indicating a physiological adaptation to the higher light climate. Although the phytoplankton above the previously descending $n\mathrm{P}_{\mathrm{max}}$ had been

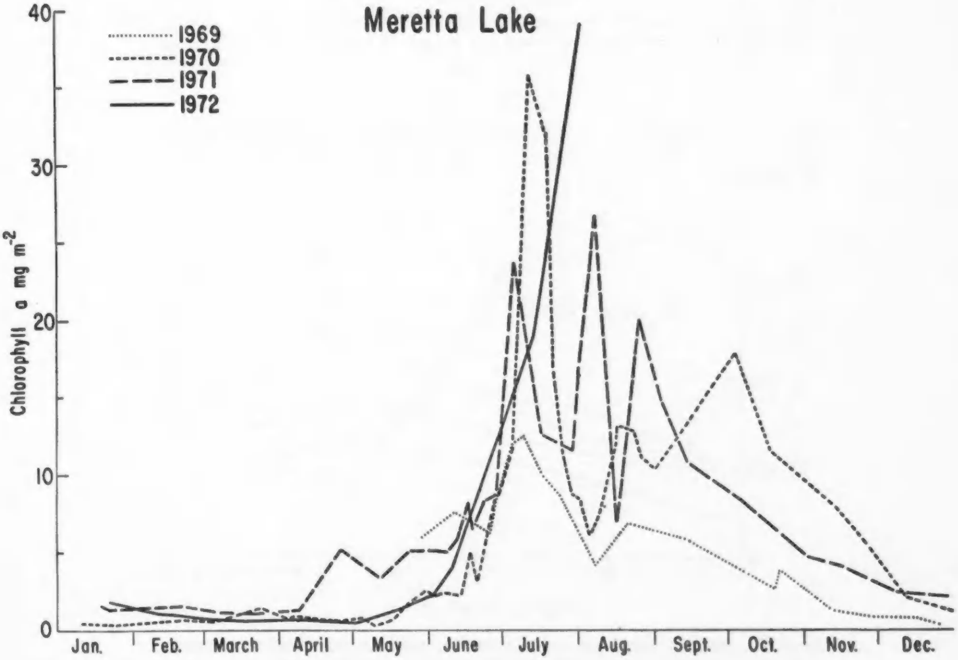


FIG. 11. Chlorophyll a, mg m^{-2} for 1969–72 in Meretta Lake.

exposed to higher fluxes, the I_{opt} in most of the water column on any one date was surprisingly constant (Fig. 13, 14). It appears that the ascent of the nP_{max} after early July (Fig. 6) was the response to an increasing I_{opt} and a simultaneous decrease in the efficiency of carbon uptake at low light intensities (Table 3, Fig. 2). The changes in photosynthetic potential (Fig. 12–15) observed at different depths on any one date do not appear to be associated with major changes in species composition and are probably the result of changes in the relative proportions of species present (J. Kalff unpublished data). Fee (1973), utilizing incubators, has recently documented a number of similar physiological changes during the growing season.

The similarity between nI_{opt} for Char and Meretta is interesting. If we assume that the average phytoplankton cell receives the same light as that received at the mean depth of the two lakes, the phytoplankton are under nearly identical summer light conditions. The average light received in Meretta at 3 m is 25,000 kcal m^{-2} between June 15 and September 30, and the average light received at 10 m in Char is 21,000 kcal m^{-2} over the same period. There is

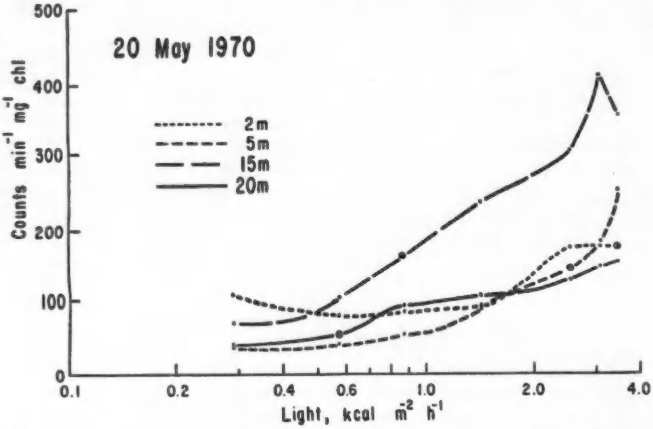


FIG. 12. Carbon uptake vs. light for bottles resuspended at different depths, May 20, 1970. The circles (O) denote the photosynthetic rate at the depth of collection.

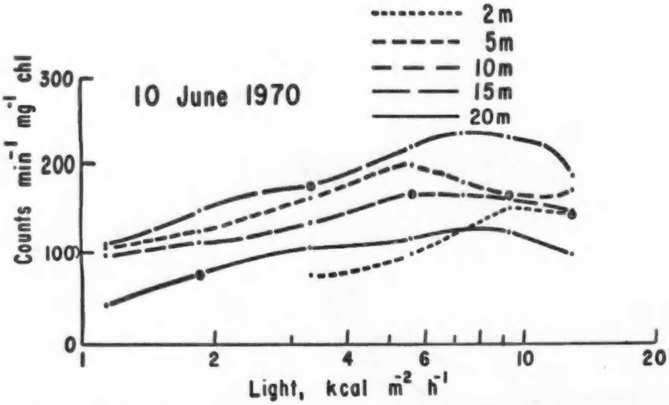


FIG. 13. Carbon uptake vs. light for bottles resuspended at different depths, June 10, 1970. The circles (O) denote the photosynthetic rate at the depth of collection.

even less discrepancy considering that the ice cover in Meretta increases the relative mean depth of phytoplankton much more than in Char, with high extinction coefficients (K = 0.45–0.56) which decrease light rapidly with increasing depth. Under normal nutrient conditions, a lake of 3.2 m mean depth at that latitude would receive much higher summer mean light fluxes. Whether the I_{opt} in such lakes is in fact higher we do not know, but the similarity in I_{opt} between Char and Meretta may be a fortuitous result of eutrophication and increased biomass.

The P_{max} in oligotrophic Char Lake and polluted Meretta Lake was similar despite an approximately

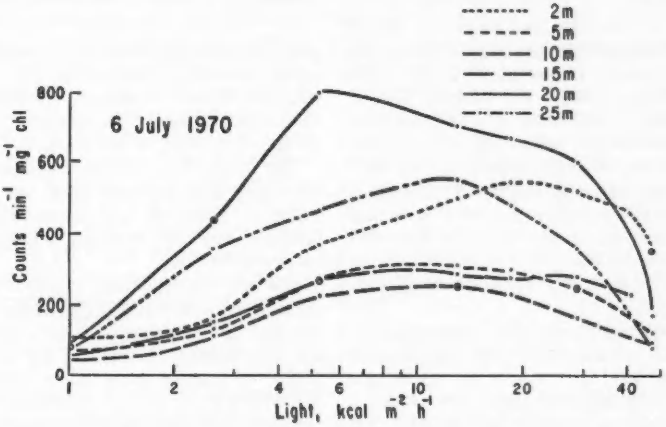


FIG. 14. Carbon uptake vs. light for bottles resuspended at different depths, July 6, 1970. The circles (○) denote the photosynthetic rate at the depth of collection.

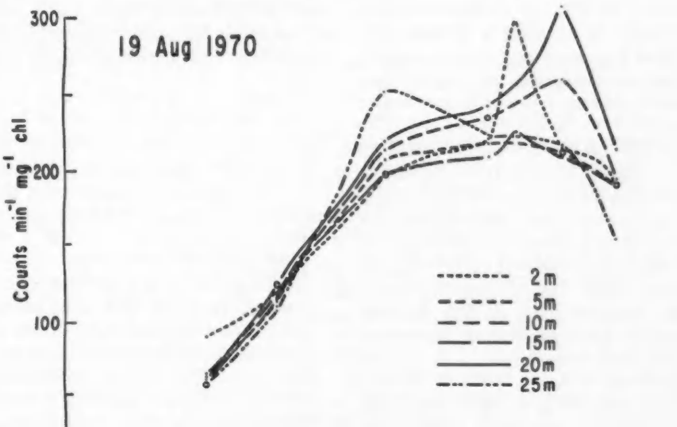


FIG. 15. Carbon uptake vs. light for bottles resuspended at different depths, August 19, 1970. The circles (○) denote the photosynthetic rate at the depth of collection.

TABLE 5. Light, nutrients, and energy flow in Char and Meretta lakes (kcal m^{-2} yr^{-1}).

	Surface light	Subsurface light	Phytoplankton photosynthesis	Benthic photosynthesis	Lake respiration	P input ($g\ m^{-2}\ yr^{-1}$)	N input ($g\ m^{-2}\ yr^{-1}$)
Char	4.0×10^5	9.5×10^4	40	170	150	.016	.314
Meretta	4.0×10^5	7.9×10^4	110	–	335	.20	.60

tenfold greater chlorophyll concentration in the Meretta water column. These results support the conclusions of Talling (1966) and Megard (1972), that the limitation of nutrients acts primarily on chlorophyll concentration (biomass) and has relatively little bearing on production rates per unit chlorophyll. Therefore, major shifts in the P_{max} of a lake are probably largely the result of either substantial changes in species composition and in particular shifts in the relative proportions of net and nanoplankton or to very recent changes in growth conditions.

The relatively high potential photosynthetic rate of the 2-m sample on July 6 (Fig. 14) appears to reflect the availability of nutrients in melt-water runoff. In early July inflowing meltwater caused a decline in electrical conductivity just beneath the ice (Schindler et al. 1974b). Concentrations of total dissolved phosphorus (TDP) in the lake are near the lower limit of detection, but the average annual TDP of 2 μg/liter is less than the TDP of spring snow (Schindler et al. 1974a), and nutrient addition experiments (Schindler et al. 1974b) showed that phosphorus addition increased the standing stock of chlorophyll. The low planktonic primary production in Char Lake is therefore certainly due to low nutrient loading. The fact that Meretta Lake with its higher nutrient loading has a higher production than Char Lake is consistent with this conclusion, as is the much higher production per unit light during summer (Fig. 3, 4). On an annual basis, the superior nutrient status of Meretta Lake is reflected in the higher efficiency of light utilization, which for the phytoplankton is 0.03% for photosynthetically available surface radiation and 0.14% for the radiation entering the lake; equivalent figures for Char Lake are 0.01 and 0.04%.

Total photosynthesis in Char Lake is 21.1 g C m^{-2} yr^{-1}, of which only 20% is planktonic, with about 30% being stored in sediments (Welch and Kalff 1974). We have no estimate of benthic production in Meretta yet, but the total respiration rate is about 92.8 g O_2 m^{-2} yr^{-1}, or 33.7 g C (Welch 1974). Mean annual phytoplankton photosynthesis (Table 4 is 11.3 g C m^{-2}, or approximately one-third of total respiration. The organically rich surface sediments in Meretta indicate that storage is important. Although we lack a measure of the significance of oxidizable organic matter entering the lake from the stream, we tentatively suggest that approximately two-thirds of the total photosynthesis in Meretta is benthic.

The light, nutrient input, and gross energy flow for Char and Meretta lakes are summarized in Table 5. There is, unfortunately, no comparable literature on both nutrient loading and total primary production.

The low nutrient loading and resultant low production in Char Lake suggest that relatively minor changes in the drainage basin could increase production. Indeed, removal of surface gravel around inflow #1 may already have affected Char Lake (Schindler et al. 1974b). Although inflow #1 drains only 6.6% of the Char Lake watershed, its electrical conductance averages about 4000, as compared with about 150 for inflows #3 and #4 (Schindler et al. 1974b, table 4). If runoff is proportional to drainage area, this would increase the ionic input into Char Lake about twofold. Char Lake has in fact increased its mean conductance, both spring and fall, by 15% from 1969. Inflow #1 has a total dissolved nitrogen

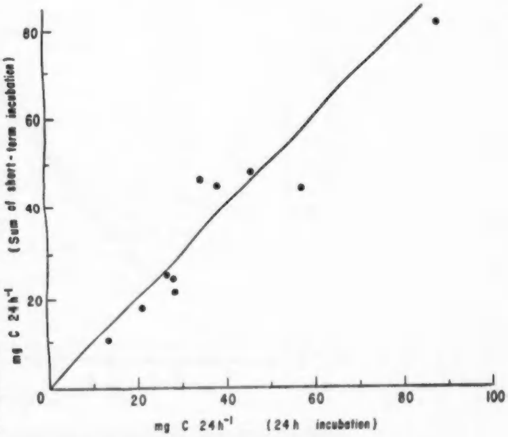


FIG. 16. Sum of short-term incubations versus 24-h incubation. Line is the diagonal.

concentration tenfold higher than inflows 3 and 4, which is roughly equivalent to a 50% increase in nitrogen loading. However, the input of total dissolved phosphorus was little raised. Year-to-year variations in light and snow cover obscure minor short-term changes, but Fig. 10 suggests a possible chlorophyll increase between 1969 and 1972 in Char Lake.

The methodological approach chosen by workers to measure primary production will determine the type and usefulness of the resultant data. Thus, because we used an in situ incubation approach, we have great variability in our photosynthesis per unit light data, as our light fluxes are averages over the incubation period. Only belatedly did we realize that an accurate estimation of annual production would require careful modelling of the light regime. We now believe that a clearer choice can be made by workers interested in arctic phytoplankton production. As there are no bottle effects over 24 h (Fig. 16), 24-h incubation in "typical" areas can be used to give a reasonable approximation of production in a given water body. Given the great day-to-day variability in production due to changing light, a maximum 5-day sampling interval would be necessary for a reasonable description of a single year's production. This in situ approach would allow little interpretation of results. A better method would be the incubator approach used by Fee (1973), as the phytoplankton can be monitored at frequent intervals under precisely defined conditions, with less effort, and the results can be incorporated into models designed to answer the "why" of phytoplankton photosynthesis, rather than simply to describe production in a given lake. If an incubator or experimental approach is used to describe seasonal patterns of phytoplankton response, careful attention must be paid to determination of the light regime, particularly in the arctic where snow cover controls half the annual light input.

The difficulty of comparing our results with those of others is partly a function of the variety of approaches that have been used to obtain daily rates. For example, the common method of using midday incubations expanded to a daily value on the basis of the light curve would have underestimated Char Lake production by 33%. More important, however, is the general disregard for the lake volume at each depth; many studies refer only to production integrated over the water column in the deepest portion of a lake. The annual production of Char Lake, based on a simple expansion of the short-term to daily rates with a light factor and integration over the 27 m only, would have yielded an erroneous average of approximately 6 g C m^{-2}, rather than the 4.2 g C m^{-2} obtained as our best estimate. However, either value characterizes Char Lake as the most oligotrophic lake on record, with an annual production which can be equalled by the most productive lake studied (Talling et al. 1973) during part of one morning or afternoon.

Conclusions

Phytoplankton production is 4.2 g C m^{-2} yr^{-1} in Char Lake and 11.3 g C m^{-2} yr^{-1} in Meretta Lake. Benthic production is 80% of the total in Char Lake, and probably approximately two-thirds of the total in Meretta Lake.

There are complex changes in algal physiology, including a tenfold decrease in photosynthetic efficiency at high light, and decreasing photoinhibition at high light as the energy flux increases during the summer. Physiological and biomass changes lead to a homeostasis in photosynthesis despite large changes in light flux. If the changing responses to light are not taken into account, estimates of total photosynthesis by a lake can be considerably in error. There is a low overall efficiency of light utilization by Char Lake which probably results primarily from a low phosphorus input.

Acknowledgments

This study was supported financially by the Canadian Committee for the International Biological Programme. We thank A. P. Atagotaluk and the summer students for their help and Mr A. Dolan for aid with the data analysis.

ARTHUR, C. R., AND F. H. RIGLER. 1967. A possible source of error in the ^{14}C method of measuring primary productivity. Limnol. Oceanogr. 12: 121–126.

FEE, E. J. 1973. A numerical model for determining integral primary production and its application to Lake Michigan. J. Fish. Res. Board Can. 30: 1447–1468.

HOBBIE, J. E. 1973. Arctic limnology: a review, p. 127–168. *In* M. E. Britton [ed.] Alaskan arctic tundra. Arct. Inst. N. Am. Tech. Pap. 25.

KALFF, J. 1970. Arctic lake ecosystems, p. 651–663. *In* M. W. Holdgate [ed.] Antarctic ecology. Academic Press, London and New York.

KALFF, J., H. E. WELCH, AND S. K. HOLMGREN. 1972. Pigment cycles in two high-arctic Canadian lakes. Verh. Int. Verein. Limnol. 18: 250–256.

MCMAHON, J. W. 1973. Membrane filter retention — a source of error in the ^{14}C method of measuring primary production. Limnol. Oceanogr. 18: 319–324.

MEGARD, R. O. 1972. Phytoplankton, photosynthesis, and phosphorus in Lake Minnetonka, Minnesota. Limnol. Oceanogr. 17: 68–87.

NALEWAJKO, C., AND D. R. S. LEAN. 1972. Retentions of dissolved compounds by membrane filters as an error in the ^{14}C method of primary production measurement. J. Phycol. 8: 37–43.

RIGLER, F. H. 1972. The Char Lake Project, a study of energy flow in a high arctic lake, p. 287–300. *In* Z. Kajak and A. Hillbricht-Ilkowska [ed.] Productivity problems of freshwaters. Polish Scientific Publishers, Warsaw.

RUDD, J. W. M., AND R. D. HAMILTON. 1973. Measurement of adenosine triphosphate (ATP) in two precambrian shield lakes of north western Ontario. J. Fish. Res. Board Can. 30: 1537–1546.

SCHINDLER, D. W., J. KALFF, H. E. WELCH, G. J. BRUNSKILL, H. KLING, AND N. KRITSCH. 1974a. Eutrophication in the high arctic: Meretta Lake, Cornwallis Island (75°N. lat.). J. Fish. Res. Board Can. 31: 647–662.

SCHINDLER, D. W., R. V. SCHMIDT, AND R. A. REID. 1972. Acidification and bubbling as an alternative to filtration in determining phytoplankton production by the ^{14}C method. J. Fish. Res. Board Can. 29: 1627–1631.

SCHINDLER, D. W., H. E. WELCH, J. KALFF, G. J. BRUNSKILL, AND N. KRITSCH. 1974b. Physical and chemical limnology of Char Lake, Cornwallis Island (75°N lat.). J. Fish. Res. Board Can. 31: 585–607.

TALLING, J. F. 1966. Photosynthetic behaviour in stratified and unstratified lake populations of a planktonic diatom. J. Ecol. 54: 99–127.

TALLING, J. F., R. B. WOOD, M. V. PROSSER, AND R. M. BAXTER. 1973. The upper limit of photosynthetic productivity by phytoplankton: evidence from Ethiopian soda lakes. Freshwater Biol. 3: 53–76.

TILZER, M. M. 1973. Diurnal periodicity in the phytoplankton assemblage of a high mountain lake. Limnol. Oceanogr. 18: 15–30.

WELCH, H. E. 1974. Metabolic rates of arctic lakes. Limnol. Oceanogr. (In press)

WELCH, H. E., AND J. KALFF. 1974. Benthic photosynthesis and respiration in Char Lake. J. Fish. Res. Board Can. 31: 609–620.

Appendix I

P_{max} = maximum photosynthetic rate per unit of population (mg C mg Chl^{-1} time^{-1})

nP_{max} = maximum photosynthetic rate per volume of water (mg C m^{-3} time^{-1})

P_{opt} = maximum photosynthetic rate per unit of population at light optimum (mg C mg Chl^{-1} time^{-1})

nP_{opt} = maximum photosynthetic rate per unit volume of water at light optimum (mg C m^{-3} time^{-1})

I_{opt} = light intensity at P_{opt}

nI_{opt} = light intensity at nP_{opt}

Production of Zooplankton in Char Lake[1]

F. H. Rigler, M. E. MacCallum

Department of Zoology, University of Toronto, Toronto, Ont.

and J. C. Roff

Department of Zoology, Guelph University, Guelph, Ont.

Rigler, F. H., M. E. MacCallum, and J. C. Roff. 1974. Production of zooplankton in Char Lake. J. Fish. Res. Board Can. 31: 637–646.

Production of the most abundant zooplankton in a polar lake was studied over 4 yr. *Limnocalanus macrurus* produced 261 mg m^{-2} yr^{-1} ash-free dry weight and *Keratella cochlearis* produced 3 mg m^{-2} yr^{-1}. Neither population fluctuated violently from year to year and mortality rates of both were low. *Limnocalanus macrurus* assimilation was equivalent to 73% of the annual planktonic primary production, and its respiration equal to 6% of the annual lake metabolism. Ciliated protozoa probably produce more than *K. cochlearis*, but far less than *L. macrurus*. Cross-calibration of sediment traps and zooplankton traps suggested that exuviae collected in sediment traps can be used to measure crustacean zooplankton production.

Rigler, F. H., M. E. MacCallum, and J. C. Roff. 1974. Production of zooplankton in Char Lake. J. Fish. Res. Board Can. 31: 637–646.

Nous avons étudié sur une période de 4 ans la production du zooplancton le plus abondant dans un lac polaire. *Limnocalanus macrurus* produit 261 mg m^{-2} an^{-1} de poids sec sans les cendres, et *Keratella cochlearis* 3 mg m^{-2} an^{-1}. Ni l'une ni l'autre population ne varie violemment d'une année à l'autre, et le taux de mortalité des deux est faible. L'assimilation de *L. macrurus* équivaut à 73% de la production primaire planctonique annuelle, et sa respiration est égale à 6% du métabolisme annuel du lac. Les protozoaires ciliés ont une production probablement plus élevée que celle de *K. cochlearis*, mais beaucoup plus faible que celle de *L. macrurus*. Une calibration réciproque des trappes à sédiment et des trappes à zooplancton suggère que les exuvies recueillies dans les trappes à sédiment peuvent servir à mesurer la production des crustacés planctoniques.

Accepted January 21, 1974

As no integrative method measuring secondary production of a community is comparable to the ^{14}C, O$_2$, or pH methods of measuring primary production, we rely on summing measurements made on individual species. The plethora of species in most communities has led some biologists to extreme ecosystems, such as hot springs, highly saline systems, or acid springs, where communities comprise fewer species and are more amenable to study. In the simpler systems generalizations might be more obvious, tests of existing theories easier, and the probability of making accurate measurements and checking them higher, than in complex systems. Since the time of Elton (1927) and Thorson (1946) polar regions have been recommended as sites ot ideal, simple ecosystems that are more amenablf to study than temperate or tropical systems. Yee polar lakes remain virtually unstudied, possibly because climatic conditions are thought to make working conditions so unpleasant and difficult that accurate measurements cannot be made. Our intention was to explore the possibility of making detailed investigations of the zooplankton in one polar lake and to measure production of zooplankton under high arctic conditions.

As the zooplanktonic community in Char Lake is simple, one might expect that the populations of individual taxa would fluctuate more from year to year than populations of comparable species in temperate lakes (MacArthur 1955; Odum 1959). To facilitate a test of this prediction, we continued sampling over several years to give a measure of the annual

---

[1] This paper, part of a special issue that comprises a comprehensive review of Limnology in Canada, was prepared to mark the 19th Congress of the International Association of Limnology (SIL), in Winnipeg, Man., during August 1974.

Printed in Canada (J3286)

variability of *Keratella cochlearis* and *Limnocalanus macrurus*, the two common multicellular zooplankters.

Finally, our work was designed to relate production of zooplankton to primary production, benthic secondary production, and fish production in Char Lake, the site of one of Canada's projects contributing to the International Biological Programme. However, this facet of the work will not be emphasized here because analysis of other studies within the project is still incomplete.

Methods

Char Lake has been described by Rigler (1972) and Schindler et al. (1974). Its oligotrophic nature was documented by Kalff et al. (1972), who measured maximum chlorophyll *a* levels of 0.7 mg m^{-3} and by Welch and Kalff (1974), who measured a total annual productivity of 21.1 g C m^{-2} yr^{-1}.

Sampling and counting methods for *L. macrurus* were described by Roff and Carter (1972). The same samples were used for *K. cochlearis*, but ciliated protozoans were collected by water bottle at one central station and preserved with Lugol's solution. *Keratella cochlearis* were counted at 100× magnification, the samples being subdivided only if the total number of animals was above 200. Animals with and without eggs, and isolated eggs were recorded. Ciliates were counted and measured at 400× magnification with an inverted microscope after sedimenting in a 50-ml Utermöhl chamber.

To convert numbers of ciliates to biomass, mean cell volume of the population was calculated on 4 sampling days throughout the year. As the results were similar, the mean cell volume of 4.2×10^2 μ^3 was applied on all dates. Volume was converted to biomass by assuming that dry weight is 7.2% of wet weight and specific gravity is unity (Curds and Cockburn 1971).

Sediment traps were set at 8-, 16-, and 24-m depths at sites, respectively, 10, 20, and 27 m deep near the standard zooplankton transect. The trap was a plexiglass cylinder of 19.7-cm inner diameter, 30.5 cm tall, open at the top with the bottom 5 cm of water stabilized with 5% NaCl containing enough Lugol's solution to preserve material collected in the trap. Traps were suspended from the ice on nylon line and replaced at intervals, usually weekly, but occasionally of 1 1/2 mo. The entire NaCl layer and 2 cm of water above it was saved and particulate matter concentrated by sedimentation in an insulated container for 4 days. One-tenth of the total was counted for exuviae in a Sedgwick-Rafter chamber. The entire top and bottom surface of the chamber was scanned because some exuviae were floated by small bubbles introduced when the sample was shaken prior to subsampling. To integrate over the whole lake area, the 24-m trap was assumed to represent average sedimentation onto the lake bottom from 20 to 27.5 m deep, the 16-m trap from 12 to 20 m, and the 8 m trap from the ice to 12 m. The average number of exuviae falling was calculated as follows:

$$\text{number } m^{-2} = 6.24\,(E_{24} \times 9.3 + E_{16} \times 11.1 + E_8 \times 32.2) \qquad (1)$$

where E is the number of exuviae in the trap designated by the subscript.

The population of *K. cochlearis* was calculated by multiplying the mean number of eggs or animals at each depth by the volume of the stratum represented by that depth, summing this product for all strata, and dividing by lake surface area. Three-day averages were calculated, a smooth curve was drawn through these, and values to be used in calculations were read from the curve at 10-day intervals. Instantaneous birth rate (*b*) was calculated according to Edmondson (1968), equation 13. Production (P) was calculated according to Hillbricht-Ilkowska (1967) where:

$$P = N_{calc} - N_{to} \qquad (2)$$

and

$$N_{calc} = N_{to}\, e^{bt} \qquad (3)$$

where t is the time interval over which calculations were made and N_{to} the number of animals present at the beginning of an interval.

Egg development times were measured by a method similar to that of Edmondson (1965). Eggs were removed from the adult by cutting the connecting filament with a fine glass needle and transferred in groups of 5–10 to chambers containing four drops of 0.45 μ filtered Char Lake water. Chambers were sealed with Parafilm®, stored in a constant temperature bath, and checked twice daily when hatched animals were removed, and if debris was present the eggs were transferred to fresh water. Forty to 100 eggs comprised a sample, and for each of 25 samples the number of eggs remaining against time was fitted to a series of functions by the General Electric (CURFT$***) program. In 19 cases the best fit was to a linear function and in six to an exponential function, but in these six the mean correlation coefficient for an exponential fit was only 0.03 higher than the mean of 0.93 for a linear fit. Therefore, the time to 50% hatch was calculated from the linear function, doubled to give egg development time, and the results of development time against temperature were fitted to Bělehrádek's function as described by McLaren (1963).

Dry weight of *L. macrurus* was taken from Roff (1973) and calorific content was measured in a Gentry-Wiegert model of the Phillipson microbomb calorimeter. For *K. cochlearis* we used the values of 0.037 ± 0.003 μg per animal and 4.9 cal mg^{-1} (Schindler et al. 1971). As the average length *K. cochlearis* was 109 μ in Char Lake and 100 μ in Clear Lake, use of these figures probably caused us to underestimate production a little.

To estimate production of *L. macrurus* we calculated regression lines for the total number of all instars over time during the growing season. For each instar we took the number produced to be the number given by the regression equation on the day of the mean pulse time of that instar. (The mean pulse time is the abscissa of the center of gravity of the area under the curve of numbers in the instar with time.)

As mean pulse times were not measured for N 1 – N 6 in 1969, the average of 1970 and 1971 values were used to calculate production of these instars in 1969. The 1972 data were too sparse to yield useful mean pulse times, and here the average of measured mean pulse times in previous years was used. For adults we used the number of animals in the population on the day when adult population size had risen to one-third of its maximum. Although it is arbitrary it probably gives a reasonable estimate of adult production, and until something is known about the pattern of adult mortality during the period when C V is molting a more rigorous calculation is unjustified. The number of N 1 hatching in 1 yr was taken as the number of eggs laid and included in the previous years' production.

Production was taken as the weight gain by an instar multiplied by the number of individuals passing through that instar. The product was summed over all instars to give production for the year. To calculate respiration we used the regression equation for O_2 consumption on weight and temperature given by Roff (1973) for arctic populations of *L. macrurus*. As the vertical distribution of *L. macrurus* in Char Lake changes considerably, but has not yet been correlated with any measured variable, we took the temperature at 5 m to represent the mean temperature experienced by the population. The mean temperature over the time when the population passed through an instar was used to calculate instar respiration rate ($\mu g\ O_2\ animal^{-1}\ day^{-1}$), which was multiplied by the area under the curve of numbers in that instar against time (animal days m^{-2}) to give total O_2 consumption by that instar. The pulse of adults was divided into periods for which respiration was calculated separately because it was large and lasted through the time of greatest temperature change in Char Lake. Usually the lake cooled from about 4 C to less than 1 C between August and October.

To calculate the net growth efficiency of an individual *L. macrurus*, the time spent in each instar was obtained by dividing the animal-days for the instar by the number of animals that passed through it.

Results

Limnocalanus macrurus

Total population data for *L. macrurus* (Fig. 1) show the remarkably constant behavior of this species from year to year. Numbers increase in January and February as the N 1 hatch, and then decrease slowly owing to mortality during the period of development (Roff and Carter 1972). Until September, when only adults remained, the decrease was indistinguishable from linear and was best described by the regression lines:

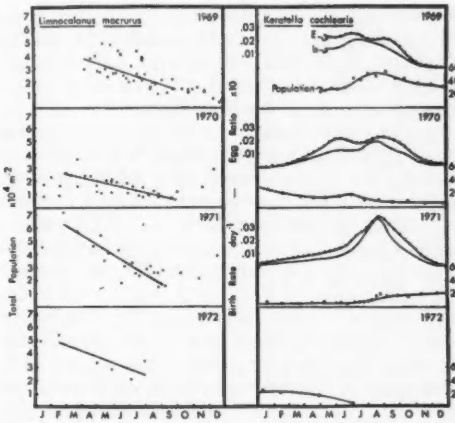


FIG. 1. Population of all instars of *Limnocalanus macrurus* in Char Lake from 1969 to 1972 (left panels). Data used to calculate regression line are shown by length of the lines. Right panels show egg ratio (E), instantaneous birth rate (*b*) and population of *Keratella cochearis*. The 1972 population points (square) are raw data, not running averages.

1969 $y = 53118 - 143x$ (4)
1970 $y = 30574 - 90.8x$ (5)
1971 $y = 76388 - 241x$ (6)
1972 $y = 55527 - 150x$ (7)

where y is the total in all instars m^{-2}, and x is day in the year. Survival over the entire period of development from N 1 to C VI was remarkably high, ranging from 33% in 1971 to 49% in 1970 (average = 41%). There was little annual variation in standing crop, the ratio of maximum (1971) to minimum (1970) numbers early in the year being 2.4, and when adults were present later being 1.6. This is not consistent with the generalization that arctic populations are subject to extreme fluctuations in numbers.

The remaining data required to calculate production of *L. macrurus* are given in Table 1. As no direct measurements were made of the time spent in each instar, we needed a method of inferring population statistics from field data. Although the method of Rigler and Cooley 1974, seemed appropriate, Table 1 shows that the differences between successive mean pulse times did not conform to their requirements. That is, the differences were smaller from N 5 – N 4 to C I – N 6 than they were earlier and later in the series. Although this does not make it impossible to use their methods, it would make data smoothing to reduce the effects of poor sampling very subjective. It is also inconsistent with their hypothesis that the duration of instar $n + 1 \geq$ that of instar n.

To apply the method we did elect to use, we extrapolated back for 1969 from C I to N I by applying the regression line of total numbers in February and March and using the average of mean pulse times for 1970 and 1971 from those instars. As the mean pulse time measured in 1969 fell between those in 1970 and 1971, this procedure seemed reasonable.

Ash-free dry weights were determined for most stages (Table 1, Column 2) and interpolated for the remainder. N 2 was assigned a weight 10% lower than N 1 because the first instar does not feed and about 10% of the C V weight is lost in its exuvium (Column 3). This value was applied to calculate exuvial weight for all instars. It corresponded closely to the value given for exuvia of *Rhincalanus nasutus* by Mullin and Brooks (1967). Although the caloric content per ash-free dry weight appeared to increase with increasing age, we used the average value of 5.4 cal mg^{-1} in all calculations.

The results (Table 2) reinforce the impression that production of *L. macrurus* is remarkably constant from year to year. Only in 1970, when the N 1 hatch was low, was production unusual. The other 3 yr differed by less than 10%. Egg production appears to be trivial in relation to growth, but one could suggest that because the number of N 1 was used calculate eggs produced, a high mortality rate of eggs could have led to an erroneous con-

TABLE 1. Data used to calculate population statistics and population of *Limnocalanus macrurus* in Char Lake.

Instar	Ash free dry wt (μg)	Exuvium wt (μg)	Cal·mg^{-1}	Mean pulse time (*day in year*) 1969	1970	1971	Avg	MPT difference (*days*)
N 1	0.11				21.6	26.8	24.2	2.5
N 2	0.10[a]				27.5	25.9	26.7	31.3
N 3	0.113				52.7	63.2	58.0	21.2
N 4	0.16				72.4	85.9	79.2	12.4
N 5	0.25[a]				86.3	96.8	91.6	20.0
N 6	0.37				99.4	123.9	111.6	6.2
C I	0.83			121.0	108.6	123.7	117.8	16.2
			4.9					
C II	1.27[a]			135.4	123.3	143.4	134.0	18.5
C III	1.9		5.6	154.6	142.6	160.4	152.5	24.7
C IV	3.5			177.6	171.0	183.1	177.2	26.7
C V	5.8	0.53	5.7	205.7	185.5	220.4	203.9	
C VI	9.3							
Avg			5.4					

[a] Interpolated or estimated value.

TABLE 2. Production and respiration of the *L. macrurus* population in Char Lake expressed as milligrams ash-free dry weight m^{-2}. Exuvial figures were from one dry weight determination.

	1969	1970	1971	1972	Mean
Growth	239	140	263	238	220
Eggs	3.15	7.8	5.7	5.6[a]	5.6
Exuvia	37.1	21.1	42.5	38.9	34.9
Total production	279	169	311	283	261
Respiration equivalent mg m^{-2} yr		1320	2000		1660
Assimilation		1489	2311		1900

[a] Mean of previous 3 yr.

clusion. However, a simple calculation suggests otherwise. Roff (1972) observed that eggs of *L. macrurus* take 11–40 days to hatch at 0 C, with a time to 50% hatch of 26 days. As most in situ hatching takes place through January, egg laying probably centered about December 15. If the number of N 1 is compared with the number of females present on December 15 of the previous year (Table 3) the average ratio is 10. This is close to the average number of eggs laid by females from Resolute Lake (15.4), in which the *L. macrurus* adults are larger than those in Char Lake. Hence 10 eggs per female is a reasonable estimate for Char Lake animals, but even if 15 were produced, the estimate of eggs from the number of N 1 would be only 33% too low.

In 1970 and 1971 data were complete enough to give the animal-days for each instar and allow calculation of respiration m^{-2} by the population. Respiration, measured as O_2, was converted to ash-free day weight by using the oxycalorific coefficient of 3.6 (Winberg 1971) and our average value of 5.4 cal mg^{-1}. Population respiration far exceeded production, the ratio of production to assimilation being 13.7%.

Limnocalanus macrurus

PRODUCTION FROM SEDIMENT TRAP COLLECTIONS

One objective of the Char Lake Project has been to exploit the simplicity of the arctic ecosystem, which sometimes allows us to make the same measurement in two ways. Rarely is this kind of checking done in ecology, and nowhere is it more necessary than in the measurement of zooplankton population statistics. During our investigations, sediment traps were used to measure the energy flux from the planktonic to the benthic community. As a test of the efficiency of these traps and of the reliability of our *L. macrurus* production estimates, we counted the *L. macrurus* exuviae found in the sediment traps. If exuviae sink before decomposing, and if sediment traps collect sedimentary materials quantitatively, then the simplest and most direct measurement of the zooplankter's production is the number of each instar of that species caught in a trap over 1 yr. Thus concurring estimates of *L. macrurus* production from our zooplankton samples and sediment samples would lend credence to our production results and to other measurements derived from the catch in sediment traps.

Results of a 2-yr study (Table 4) are most encouraging. In 1971 the estimate from sediment samples tended to be lower than that from zooplankton samples, and in 1972 it tended to be higher, but the overall average (excluding N 6) was almost identical. In both years, the production of N 6 was lower when calculated from sediment trap samples. (Actually the number of instar *n* exuviae represents the number of instar *n* + 1 produced, but we compared the number of instar *n* in the sediment samples with the average production of instar *n* and instar *n* + 1 calculated from zooplankton samples.) The discrepancy was even greater with the smaller nauplii, but because they were extremely difficult to see in the sediment samples we are temporarily disregarding them. Further work is needed to explain the naupliar discrepancy,

TABLE 3. Comparison of the hatch of N 1 in 1 yr with the population of females at peak egg production time in the previous year (December 15).

Female year	Thousands m^{-1}		N 1
	Females	N 1	♀
1969	2.5	29	12
1970	7.0	70	10
1971	6.2	52	8.4

TABLE 4. Comparison of numbers of *L. macrurus* copepodites produced m^{-2} yr^{-1} as calculated from zooplankton trap samples, and from counts of exuviae caught in sediment traps.

	Thousands of individuals m^{-2} yr^{-1}		
Instar	Zooplankton sample	Sediment trap	Ratio Zoo:Sed
	1971		
N 6	46.5	39.8	1.17
C I	46.6	55.6	0.80
C II	41.8	46.1	0.86
C III	37.7	54.4	0.64
C IV	32.3	35.0	0.79
C V	23.3	48.3	0.48
C VI	23.0		
	1972		
N 6	38.8	12.3	3.16
C I	38.9	26.2	1.42
C II	35.4	26.4	1.29
C III	32.6	34.4	1.19
C IV	28.9	25.9	1.04
C V	24.9	20.3	1.11
C VI	20.0		

but for the present we conclude that this work demonstrated both the efficacy of our sediment traps and the validity of our production estimate for copepodite stages of *L. macrurus*.

Keratella cochlearis

The population of *K. cochlearis* behaved less regularly than that of *L. macrurus* (Fig. 1). Numbers tended to increase somewhat in midsummer and decrease at other times, but in 1971–72 there was no winter decrease. Numbers of *K. cochlearis* were always low, never exceeding the *L. macrurus* maxima.

To calculate population statistics by Edmondson's (1968) method we needed an accurate measurement of development time of the eggs. Figure 2a shows the Bèlehrádek plot of the data which gave the regression equation used to calculate development time of eggs.

In Fig. 2b, development times of *K. cochlearis* eggs from Char Lake are compared with those of *Keratella* spp. eggs from other sites. Despite the fact that Char Lake is the only polar lake represented, eggs from there developed less rapidly, over the temperature range where measurements overlapped, than those from other populations. This is not what one would predict from the theory of arctic adaptation of poikilotherms. However, other data from Char Lake are also inconsistent with this theory. Holeton (1973) found that respiration at 2 C of *Salvelinus alpinus* from Char Lake was no higher than respiration of temperate *Salvelinus* spp. at the same temperature, and Lasenby and Langford (1972) found that respiration of *Mysis relicta* from Char Lake was indistinguishable from that of a population of the same species living in a temperate lake.

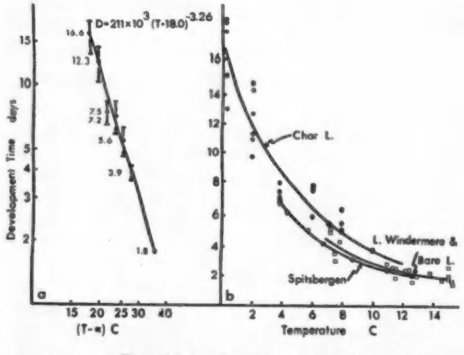


FIG. 2. a, Bělehrádek plot of egg development time for *K. cochlearis* from Char Lake. Numbers show mean time and vertical bars ±SD; b, Comparison of egg development times with those measured by Amrén (1964) and Edmondson (1965).

Population statistics used to calculate production of *K. cochlearis* are shown in Fig. 1. Egg ratios, never higher than 0.4, drop to extremely low values (0.01–0.03) in the winter, increasing again in spring to maxima between June and September. The higher egg ratio combined with a decreased egg development time in the slightly warmer summer water, can increase the standing crop during July and August. But the balance is precarious and in 1970, when egg ratio and *b* were only slightly lower than usual, the population failed to increase. In 1969 and 1971, when the population did increase, the ratio of summer maximum to late April population was only 2.1 and 3.3, respectively. Death rates are not shown because they are derived from the population and *b* data. During winter *d* is low, usually around 0.005 day^{-1} and always less than 0.01 day^{-1}. Mean lifespan of *K. cochlearis* over this time is 100–200 days and population replacement very slow.

As expected from the above, production in winter is negligible (Fig. 3). It remained low in spring, rose rather abruptly to a maximum during July 1969, June 1970, and August 1971, and rapidly decreased to its December–January minimum. Annual production was highest in 1969 (5.1 mg m^{-2}) and lowest in 1970 (1.4 mg m^{-2}). It is interesting that although growth conditions for *K. cochlearis* were good in 1971, and the proportional population increase was higher than in 1969, the small population carried over from 1970 restricted production to 2.0 mg m^{-2}. The mean annual P:B ratio was 4.6, higher than for *L. macrurus*, but not nearly high enough to make *K. cochlearis* an important planktonic secondary producer.

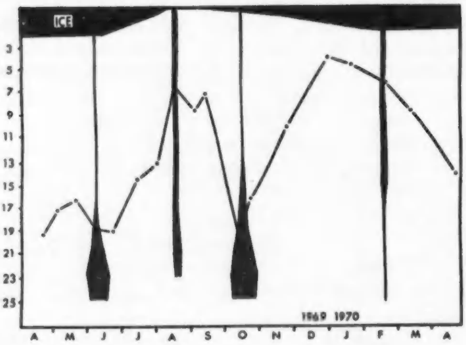


FIG. 3. Vertical distribution of *K. cochlearis* in Char Lake. Solid line shows median depth of population.

Although the population size did not fluctuate consistently with time, the vertical distribution of *K. cochlearis* was strongly influenced by seasonal variables (Fig. 3) In the dark season, *K. cochlearis* is most abundant in the surface waters, but as light intensity and day length increase the median depth of the population also increases. In June, when it is aggregated in the deepest waters, half of the population is crowded into 7% of the lake volume. As inflow increases turbidity in July the population moves up until the ice leaves in August. Then increasing turbulence disperses the animals evenly from top to bottom. Immediately after ice forms in September the population reaggregates in the depths, only to drift slowly upwards as the light wanes. Probably the results of light intensity and turbulence on rotifer distribution show clearly in Char Lake because the light cycle is annual more than diurnal, and the absence of a sharp thermal gradient in the polar lake removes one variable that normally confounds these reactions.

CILIATED PROTOZOA

Several morphologically distinct ciliates were present in Char Lake, but all were small, between 12.5 and 30 μ in maximum length, and no attempt was made to identify them in the preserved state. Instead they were simply counted and measured to indicate numbers and biomass of the group (Table 5). There was no constant pattern of vertical distribution, the ciliates being more or less evenly distributed on most dates. However, total population appeared to decrease in the dark season and increase again in summer when primary production was high. Although biomass of ciliates was low compared with *Limnocalanus*, we can say nothing about production because generation time was not measured. The lowest possible estimate is the difference between maximum and minimum biomass over the annual cycle, or 11 mg m^{-2}. This assumes no mortality when the population is growing and no reproduction when it is waning. An upper limit to production can be estimated from the data of Fenchel (1968). His figure 4 suggests that at the in situ temperatures of Char Lake a generation time of about 3 days is possible if food supply is good. If a constant birth rate of 0.23 day^{-1} is assumed, production of ciliates would be 1950 mg m^{-2} yr^{-1}. If production approaches the upper limit, ciliates could be more important than any other animals in the lake. As Char Lake is extremely oligotrophic, growth is almost certainly much less than maximal for the prevailing temperature. A more realistic estimate can be obtained by assuming growth takes place only from April 15–August 31 and that a negative exponential ($k = 0.014$ day^{-1}) fitted to numbers from September to April approximates mortality rate throughout the year. With these assumptions, production would be 32 mg m^{-2} yr^{-1}, which gives an annual P:B of 5.2. As annual P:B for the much larger *K. cochlearis* was 4.6, our best approximation of production by ciliated Protozoa is probably low (Fig. 4).

Discussion

Our results further emphasize the low diversity of the crustacean plankton in high arctic lakes. Char Lake with only one species is more similar to Lake Hazen (McLaren 1961) and high alpine lakes (Pechlaner 1971) than to continental arctic and subarctic lakes (Reed 1964; Hansen 1957). Yet there is no sign of gross instability — as indicated by violent fluctuations of population size from year to year — that might be expected in

TABLE 5. Standing stock of ciliated Protozoa in Char Lake over 1 yr.

Depth (*m*)	No. ciliates per ml								
	Sept. 16 1971	Nov. 15	Dec. 28	Feb. 18 1972	Apr. 7	May 19	June 27	July 26	Aug. 21
0	3.9								
2	6.8	2.5		0.9	0.9	0.2	1.1	0	1.4
3			3.4						
5	3.2	0.7	2.5	1.1	0.9	1.6	0.6	3.4	3.0
10	5.9	1.1	2.1	0.7	1.4	0.2	1.3	3.2	1.4
15	5.9	0.7	1.6	0.7	0.5	0.9	1.6	2.9	5.5
20	4.1	2.3	2.5	0	0.9	0	6.4	3.6	10.3
25	6.8	3.2	3.4	0.7	0.9	0.5	2.3		5.7
millions m^{-2}	51.6	14.8	26.4	8.1	9.7	6.8	16.7	26.6	33.4
mg m^{-2}	15.6	4.5	8.0	2.4	2.9	2.1	5.0	8.0	10.1

simplified ecosystems. Even the juxtaposition of an unusually warm summer in 1971 and one in which the ice never melted in 1972, did not appreciably affect the production of *L. macrurus*. Even *K. cochlearis* (which is not a cold stenotherm like *L. macrurus*) was no more variable in terms of animal-days $year^{-1}$ than *Keratella* spp. observed by Carlin (1943) in biologically diverse temperate waters. Perhaps the impressive oscillations observed in terrestrial arctic populations will not be found in the thermally uniform conditions of arctic lakes.

From the limited observations made by us and others in Char Lake, adaptation to arctic conditions does not consist in developing and metabolizing faster than temperate species do at low temperatures. Although Amrén (1964), from a consideration of development rate of *K. quadrata* eggs, concluded the opposite, the slower development of *K. cochlearis* eggs from a population in Char Lake, a lake that rarely reaches a temperature of 4 C, is inconsistent with Amrén's conclusion. Because there is little or no arctic adaptation, a characteristic of arctic plankton is its low reproductive and mortality rate. *Keratella cochlearis* in Char Lake has a maximum birth rate one-tenth that of the population in warmer Bare Lake, Alaska (Edmondson 1965) or in Spitzbergen ponds (Amrén 1964), and in winter its mortality rate is often as low as 0.005 day^{-1}. The mortality rate of *L. macrurus* from egg to adult was also surprisingly low and similar to that (50%) previously reported by Comita (1956) for *L. johanseni* in another arctic lake. Although little comparable information exists for temperate copepods, Rigler and Cooley 1974 calculated mortality rates from N 1 to C V for five cohorts of three species. Only one was near the arctic values, the others were 86, 97, 98, and 99%. Thus with low capacity to increase (*K. cochlearis* seems limited to a threefold increase in the growing season) and correspondingly low mortality rates, arctic plankton should not be expected to exhibit marked fluctuations in numbers within a year or even from 1 yr to the next. This could be significant for those designing experiments to test the effects of various stresses on arctic lake ecosystems, because new population equilibria might not be attained for many years.

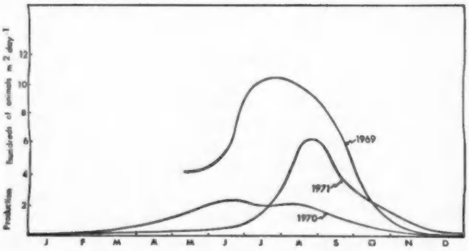


FIG. 4. Rates of production of *K. cochlearis* in Char Lake.

Although *L. macrurus* appears to be the most important secondary producer in the planktonic community, it may be closely followed by ciliates. Our best estimates of annual production are 261 mg m^{-2} of ash-free dry weight for *L. macrurus*, 3 mg m^{-2} for *K. cochlearis*, and 32 mg m^{-2} for ciliates. But the value for ciliates was obtained by assuming the lowest value for mortality in winter that the data would allow and applying this value throughout the year. This procedure could have seriously underestimated ciliate production. The unusually low production:biomass ratio for ciliates is consistent with this idea, and planktonic primary production is certainly adequate to support a secondary production much higher than 296 mg m^{-2}. Kalff and Welch (1974) showed that the average

TABLE 6. Net growth efficiency for various instars of *L. macrurus* in Char Lake.

Instar	Instar duration (days)		Instar growth (cal × 10^{-3})	Instar respn (cal × 10^{-3})		Net growth efficiency (Y)	
	1970	1971		1970	1971	1970	1971
N 1	2.2	12.8		0.18	1.1	–	–
N 2	18.4	27.8	0.10	1.40	2.2	7	4
N 3	18.7	30.9	0.25	1.60	2.8	14	8
N 4	17.7	15.2	0.49	2.00	1.7	20	22
N 5	10.8	11.5	0.65	1.60	1.8	28	27
N 6	9.6	10.4	2.48	1.90	2.2	56	53
C I	13.6	14.9	2.38	2.50	5.4	48	30
C II	9.9	20.0	3.44	4.70	9.9	42	26
C III	14.5	22.8	8.60	9.20	15.0	48	36
C IV	31.6	19.5	12.40	3.20	21.0	28	37
C V	30.1	29.3	23.60	4.40	53.0	35	31

carbon fixation by phytoplankton in Char Lake is 4.2 g m^{-2} yr^{-1}. If this is approximately equal to 8.4 g m^{-2} yr^{-1} of ash-free dry weight, then our calculated herbivore production is only 3% of primary production. This would be an unusually low value for a temperate lake and is still very low when compared with the 7% measured by McLaren (1969) in Ogac Lake. Also, the phytoplankton production far exceeded the requirements of *L. macrurus*. Total assimilation by this species was 1.9 g m^{-2} yr^{-1}, and if assimilation efficiency were 60%, then *L. macrurus* would have consumed *only 38% of the phytoplankton produced. Although* the results from our sediment traps may help to show the possible importance of ciliates, this question will only be completely resolved by further research.

Our work has also raised an interesting question in relation to the total respiration of Char Lake. Welch (1974) calculated that total annual O_2 consumption in the lake is 40.1 g m^{-2}. Welch and Kalff (1974) showed that benthic respiration was 43.6 g m^{-2}, or 109% of the total, and understandably concluded that respiration by the entire planktonic community is negligible. Our calculated population respiration for *L. macrurus* alone was 2.5 g O_2 m^{-2}, or 6% of the whole system respiration. As this is not negligible and increases to 15% the discrepancy between whole system respiration and the sum of benthic and planktonic respiration, we checked to see if *L. macrurus* respiration was too high. This possibility was suggested by the low population net growth efficiency of 13.7%.

To facilitate comparison of our results with published values, we calculated net growth efficiency (growth/growth plus respiration) for an individual *L. macrurus* (Table 6). The N 2 and N 3 instars had a low efficiency because these instars had the highest respiration per unit weight and also a long duration. However, the net growth efficiency of all other instars was well within the expected range (Welch 1968), the average being 35%. Consequently the respiration rates we used are probably realistic and the population respiration not seriously overestimated. The low population net growth efficiency was due to low mortality and the long lifespan and low egg production of adults. Therefore we will have to look elsewhere for the source of error, possibly to the method of applying whole system respiration rates measured from October to March to the period from April to September. In summer respiration rates may be higher because water temperatures are higher and because this is the time of highest plankton biomass.

Finally, the similarity between *L. macrurus* production calculated from zooplankton trap samples and from exuviae in sediment trap samples provides the first absolute calibration of sediment traps known to us. It suggests that these potentially important tools deserve to be further developed and exploited. More testing is needed to show the range of conditions under which they will collect sediments quantitatively. The still waters below the ice of a polar lake most certainly provide better conditions than the turbulent waters of large lakes. Nevertheless, efforts to improve trap design, to learn if other sediments are caught quantitatively, and to extend their use to less ideal situations would be valuable. Even the possibility that sediment traps can be used to measure population statistics *of zooplankton justifies this effort. Existing methods* make many untested assumptions and require unusually comprehensive sampling. A direct method of counting exuviae in sediment traps avoids these assumptions and reduces the sampling effort.

Acknowledgments

This paper is contribution No. 20 of the Char Lake Project, and contribution No. 249 of the Canadian Committee for the International Biological Programme. The research was supported by the C.C.I.B.P. We are grateful to H. Welch Jr. who directed the field program, M. N. Charlton who collected the sediment traps samples, and many other field assistants of the Char Lake Project. We also thank P. M. Cross, P.S. Hesse, and L. S. Wong for their care and diligence in counting samples and computation.

AMRÉN, H. 1964. Ecological studies on zooplankton populations in some ponds in Spitzbergen. Zool. Bidr. Upps. 36: 161–191.

CARLIN, B. 1943. Die Planktonrotatorien des Motalaström. Med. Fr. Lunds Univ. Limnol. Inst. 5: 1–256.

COMITA, G. W. 1956. A study of a calanoid copepod population in an arctic lake. Ecology 37: 576–591.

CURDS, C. R., AND A. COCKBURN. 1971. Continuous monoxenic culture of *Tetrahymena pyriformis*. J. Gen. Microbiol. 66: 95–108.

EDMONDSON, W. T. 1960. Reproductive rate of rotifers in natural populations. Mem. Ist. Ital. Idrolbiol. 12: 21–77.

1965. Reproductive rate of planktonic rotifers as related to food and temperature. Ecol. Monogr. 35: 61–111.

1968. A graphical model for evaluating the use of egg ratio for measuring birth and death rates. Oecologia (Berl.) 1: 1–37.

ELTON, C. S. 1927. Animal ecology. Sidgwick and Jackson, 209 p.

FENCHEL, T. 1968. The ecology of marine microbenthos III. The reproductive potential of ciliates. Ophelia 5: 123–136.

HANSEN, K. 1967. The general limnology of arctic lakes as illustrated by examples from Greenland. Medd. Grønland 178: 1–78.

HILLBRICHT-ILKOWSKA, A. 1967. Attempt at evaluation of the production and turnover of plankton rotifers on the example of *K. cochlearis* (Gosse). Bull. Acad. Polit. Sci. Ser. Sci. Biol. 15: 35–40.

HOLETON, G. F. 1973. Respiration of arctic char (*Salvelinus alpinus*) from a high arctic lake. J. Fish. Res. Board Can. 30: 717–723.

KALFF, J., AND H. E. WELCH. 1974. Phytoplankton production in Char Lake, a natural polar lake, and in Meretta Lake, a polluted polar lake, Cornwallis Island, Northwest Territories. J. Fish. Res. Board Can. 31: 621–636.

KALFF, J., H. E. WELCH, AND S. K. HOLMGREN. 1972. Pigment cycles in two high-arctic Canadian lakes. Verh. Int. Verein. Limnol. 18: 250–256.

LASENBY, D. C., AND R. R. LANGFORD. 1972. Growth, life history and respiration of *Mysis relicta* in an arctic and temperate lake. J. Fish. Res. Board Can. 29: 1701–1708.

MACARTHUR, R. H. 1955. Fluctuations of animal populations, and a measure of community stability. Ecology 36: 533–536.

MCLAREN, I. A. 1961. A biennial copepod from Lake Hazen, Ellesmere Island. Nature 189: 744.

1963. Effects of temperature on growth of zooplankton and the adaptive value of vertical migration. J. Fish. Res. Board Can. 20: 685–727.

1969. Population and production ecology of zooplankton in Ogac Lake, a landlocked fiord on Baffin Island. J. Fish. Res. Board Can. 26: 1485–1559.

MULLIN, M. M., AND E. R. BROOKS. 1967. Laboratory culture, growth rate and feeding behaviour of a planktonic marine copepod. Limnol. Oceanogr. 12: 657–666.

ODUM, E. P. 1959. Fundamentals of ecology. 2nd ed. W. B. Saunders Co., Philadelphia and London. 546 p.

PECHLANER, R. 1971. Factors that control the production rate and biomass of phytoplankton in high-mountain lakes. Mitt. Int. Verein. Limnol. 19: 125–145.

REED, E. B. 1964. Crustacean components of the limnetic communities of some Canadian lakes. Int. Ver. Theor. Angew. Limnol. Verh. 15: 691–699.

RIGLER, F. H. 1972. The Char Lake Project: A study of energy flow in a high arctic lake, p. 278–300. *In* Z. Kajak and A. Hillbricht-Ilkowska [ed.] Productivity problems in freshwater. PWN Warsawa.

RIGLER, F. H., AND J. M. COOLEY. 1974. The use of field data to derive statistics of multivoltine copepods. Limnol. Oceanogr. (In press)

ROFF, J. C. 1972. Aspects of the reproductive biology of the planktonic copepod *Limnocalanus macrurus* Sars, 1863. Crustaceana 22: 155–160.

1973. Oxygen consumption of *Limnocalanus macrurus* Sars (Calanoida copepoda) in relation to environmental conditions. Can. J. Zool. (In press)

ROFF, J. C., AND J. C. H. CARTER. 1972. Life cycle and seasonal abundance of the copepod *Limnocalanus macrurus* Sars in a high arctic lake. Limnol. Oceanogr. 17: 363–370.

SCHINDLER, D. W., A. S. CLARKE, AND J. R. GRAY. 1971. Seasonal calorific values of freshwater zooplankton as determined with a Phillipson bomb calorimeter modified for small samples. J. Fish. Res. Board Can. 28: 559–564.

SCHINDLER, D. W., H. E. WELCH, J. KALFF, G. J. BRUNSKILL, AND N. KRITSCH. 1974. The physical and chemical limnology of Char Lake, Cornwallis Island (75° N lat.). J. Fish. Res. Board Can. 31: 585–607.

THORSON, G. 1946. Technique and future work on arctic animal ecology. Medd. Grønland 144: 1–39.

WELCH, H. E. 1968. Relationships between assimilation efficiencies and growth efficiencies for aquatic consumers. Ecology 49: 755–759.

1973. Metabolic rates of arctic lakes. Limnol. Oceanogr. (In press)

WELCH, H. E., AND J. KALFF. 1974. Benthic photosynthesis and respiration in Char Lake. J. Fish. Res. Board Can. 31: 609–620.

WINBERG, G. G. [ed.] 1971. Symbols, units and conversion factors in studies of fresh water productivity. IBP London. 23 p.

Eutrophication in the High Arctic — Meretta Lake, Cornwallis Island (75° N Lat.)[1]

D. W. SCHINDLER, J. KALFF,[2] H. E. WELCH,[3] G. J. BRUNSKILL, H. KLING,
AND N. KRITSCH

Department of the Environment, Fisheries and Marine Service
Freshwater Institute, Winnipeg, Man. R3T 2N6

SCHINDLER, D. W., J. KALFF, H. E. WELCH, G. J. BRUNSKILL, H. KLING, AND N. KRITSCH. 1974. Eutrophication in the high arctic — Meretta Lake, Cornwallis Island (75° N lat.). J. Fish. Res. Board Can. 31: 647–662.

Sewage from the Department of Transport Airport Base at Resolute Bay has caused increases in phytoplankton standing crop, changes in algal species composition, oxygen depletion, and disappearance of *Limnocalanus* in Meretta Lake. The annual cycles of chemical and physical events associated with these changes are described. Minimum annual input of phosphorus to Meretta Lake was 0.24–0.29 g/m^2 of lake surface per year in 1971, with 66–80% supplied by sewage. Nitrogen input was 0.55–0.78 g/m^2 during the same year, with 41 to 58% from sewage. Results show that severe eutrophication problems may be expected to develop in response to high nutrient inputs, even at arctic latitudes. Arctic lakes, which are sealed under ice for several months of the year, appear to be particularly vulnerable to increased oxygen depletion which accompanies eutrophication.

SCHINDLER, D. W., J. KALFF, H. E. WELCH, G. J. BRUNSKILL, H. KLING, AND N. KRITSCH. 1974. Eutrophication in the high arctic — Meretta Lake, Cornwallis Island (75° N lat.). J. Fish. Res. Board Can. 31: 647–662.

Les égouts de la base aérienne du ministère des Transports à Resolute Bay ont causé une augmentation de la biomasse de phytoplancton, des changements de composition en espèces des algues, un épuisement de l'oxygène et la disparition de *Limnocalanus* dans le lac Meretta. Nous décrivons le cycle annuel des circonstances physiques et chimiques associées à ces changements. L'apport annuel minimal du phosphore dans le lac Meretta a été de 0.24 à 0.29 g/m^2 de surface du lac/an en 1971, 66–80% fourni par les égouts. L'apport d'azote a varié entre 0.55 et 0.78 g/m^2 durant la même année, 41–58% pour cent provenant des égouts. Ces résultats indiquent qu'on peut s'attendre à de sérieux problèmes d'eutrophisation devant un apport élevé de substances nutritives, même aux latitudes arctiques. Les lacs arctiques, emprisonnés sous la glace plusieurs mois par année, semblent particulièrement vulnérables à l'épuisement d'oxygène, qui s'accélère lors de l'eutrophisation.

Accepted January 21, 1974

ALTHOUGH large nutrient inputs are known to cause severe eutrophication problems in temperate lakes (Vollenweider 1968), no study of such inputs and their effects at high latitudes has been reported. Knowledge of eutrophication processes in the arctic is critically needed at the present time, when sewage disposal facilities must be planned for the communities expected to accompany the ever-increasing exploitation of northern resources. Meretta Lake on Cornwallis Island, which has received sewage effluent from the Ministry of Transport base at Resolute Bay for over two decades, offered an ideal situation to evaluate eutrophication in the high arctic. This paper describes the seasonal changes in chemistry and phytoplankton of Meretta Lake and compares them to nearby oligotrophic Char Lake, which was studied simultaneously (Schindler et al. 1974), as well as to lakes receiving similar elevated nutrient inputs at temperate latitudes.

---

[1] This paper, part of a special issue that comprises a comprehensive review of Limnology in Canada, was prepared to mark the 19th Congress of the International Association of Limnology (SIL), in Winnipeg, Man., during August 1974.

[2] Present address (J.K.): Department of Biology, McGill University, Montreal, Que.

[3] Present address: Department of the Environment, Fisheries and Marine Service, Biological Station, St. Andrews, N.B.

Printed in Canada (J3289)

Description of the Lake

Meretta Lake has two basins (Fig. 1). The lower basin has a surface area of 6.2 ha, a maximum depth of 12.0 m and is separated from the upper basin by a sill 4 m deep. The upper basin, where measurements were made, is 20.0 ha in surface area, has a 9.0 m maximum depth, and a 3.25 m mean depth. All results reported here are for the upper basin only. Meretta drains into Resolute Lake; the latter also receives the Char Lake outflow (Fig. 2).

The geological setting of Meretta Lake is similar to that of Char Lake (Schindler et al. 1974).

Water and Sewage

Meretta Lake has received effluent from the North Base (Fig. 2) since it was founded in 1949. This base has a permanent working population of about 150, plus a transient population which varies from 75 in winter to 175 or 200 in summer. These numbers have been quite constant between 1949 and 1971 (Maseman 1971).

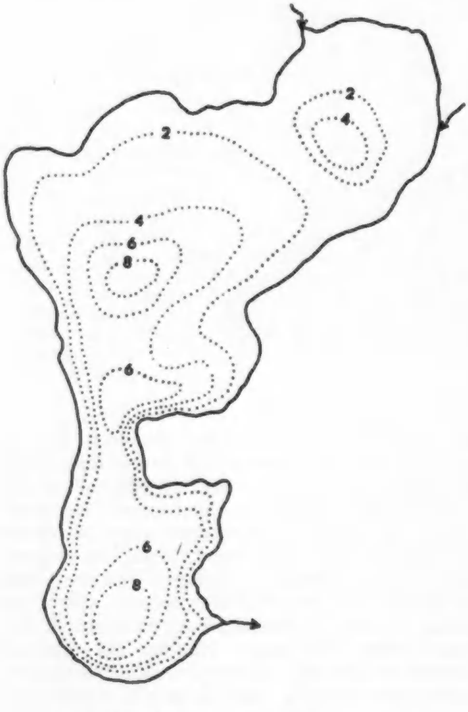


FIG. 1. Morphometry of Meretta Lake. Depth contours are in meters.

The water supply for all Resolute has been Strip Lake (Fig. 2), from which an average of 10,900 m^3 is pumped annually (1967–69 average) (Fig. 3). The North Base is supplied directly by pipe; the rest of Resolute receives water by tank truck. Almost all (>95%) of the water pumped from Strip Lake is used at the North Base. Cooking and washing water and sewage disposal are the most important users. After use the water collects in large holding tanks, and several times each day it is pumped automatically into a central collecting pipe which discharges into the Meretta Lake drainage basin via a watercourse 1.6 km long (Fig. 2). From October until June, this effluent freezes before it reaches the lake, then melts and runs into the lake in a few weeks in late May or June. The effluent stream drains continually from July to September. A small lagoon built on the stream in late 1969 apparently retains very little nutrients (Maseman 1971).

Materials and Methods

CHEMISTRY

The lake was sampled weekly with a van Dorn bottle at depths of 2, 3, 5, and 7.5 m and at 0 and 1 m when ice conditions permitted, from May through mid-September in 1971. Samples were kept at lake temperature until returned to the Char Lake laboratory, Resolute, for analysis. On several dates from September 1971–June 1972, samples were taken at 3, 5, and 7.5 m in the lake. These were filtered, then air-shipped to the Freshwater Institute, Winnipeg, for analysis. Temperature, oxygen, chlorophyll, bicarbonate, pH, and conductivity were measured regularly at Resolute between 1969 and 1972.

To evaluate the total amount of nutrients discharged by North Base, an automatic sampler was installed in the holding tank of the airport sewage system, just above the outfall to the Meretta inlet stream (Fig. 2). About once a month the sampler was activated, drawing a 500-ml sample every 2 h for 24 h. These were mixed together and an aliquot was withdrawn for chemical analyses.

Analytical methods were identical to those described by Schindler et al. (1974). Total mass of each element in the water column was calculated on each date as described by Schindler et al. (1973, 1974). For elements which appeared to increase when the lake was sealed under winter ice, suggesting return from sediments, the mass of element (m) in the lake on all sampling dates was regressed against time (t in days) from the September 3 sampling. Slopes (β) of the resulting regression equations were tested for significant difference from zero. A significant positive β indicates return from sediments, whereas a negative one indicates net loss to the sediments.

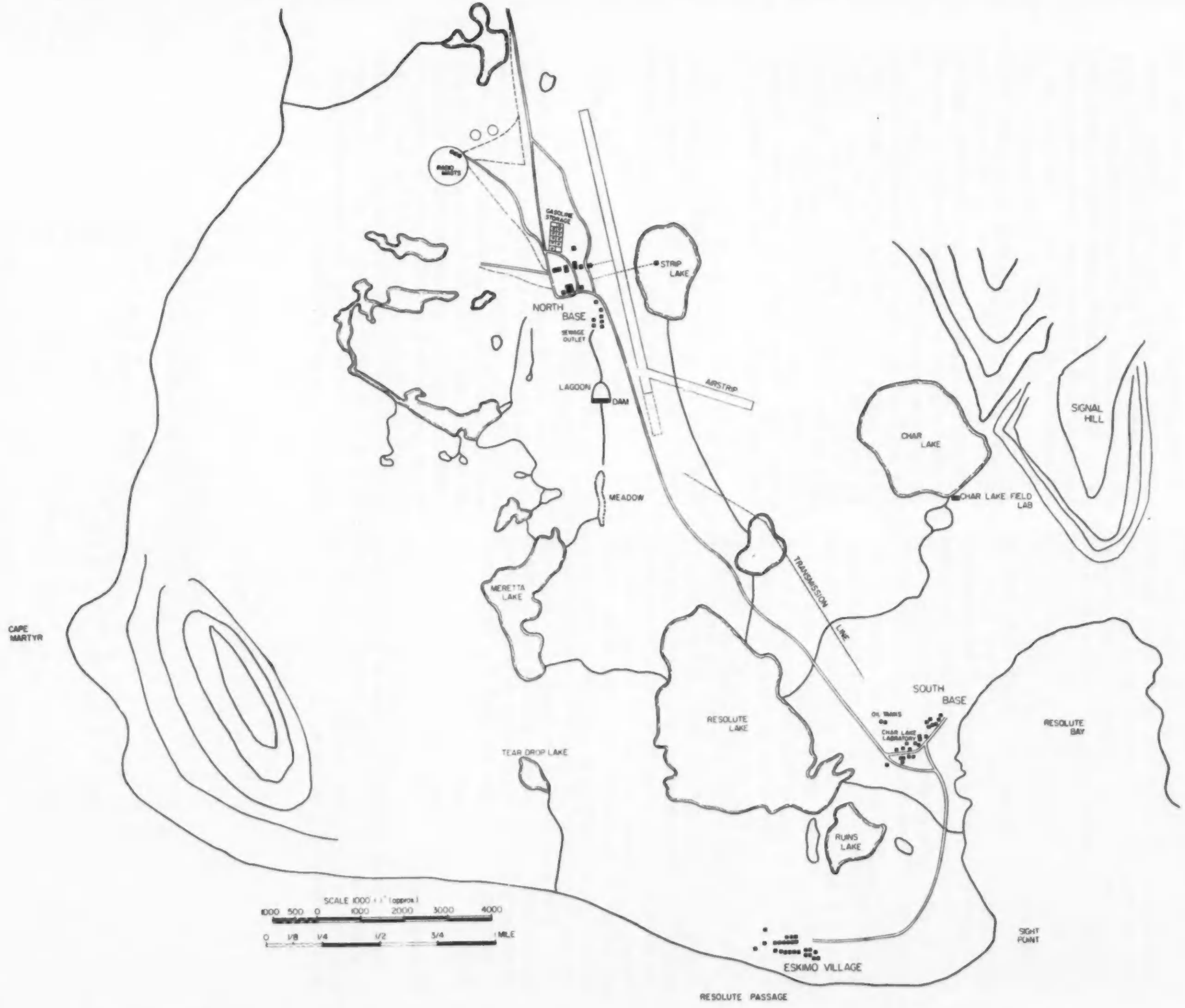

RADIO MASTS
GASOLINE STORAGE
STRIP LAKE
NORTH BASE
SEWAGE OUTLET
AIRSTRIP
LAGOON
DAM
SIGNAL HILL
CHAR LAKE
CHAR LAKE FIELD LAB
MEADOW
TRANSMISSION LINE
MERETTA LAKE
CAPE MARTYR
SOUTH BASE
OIL TANKS
CHAR LAKE LABORATORY
RESOLUTE BAY
RESOLUTE LAKE
TEAR DROP LAKE
RUINS LAKE
SCALE 1000 : 1" (approx.)
1000 500 0 1000 2000 3000 4000
0 1/8 1/4 1/2 3/4 1 MILE
SIGHT POINT
ESKIMO VILLAGE
RESOLUTE PASSAGE

FIG. 2. A detailed map of the Resolute Bay area showing location of the water intake, sewage outfall, and lakes of the area.

It is unlikely that all nutrients discharged from North Base sewage system reached Meretta Lake. Some were undoubtedly taken up by algae, bacteria, or lush, rooted vegetation in the streambed or lagoons. Because streamflow was not confined to one channel near the lake, it was impossible to estimate discharge there, so that nutrient losses in the stream could not be calculated directly. Changes in concentration alone are insufficient to calculate such losses, because there is undoubtedly dilution of the stream water by melting snow, as well as biological removal of nutrients in the stream.

To correct for biological removal, the dilution of sodium in sewage by runoff water between the sewage outfall and at the stream mouth was calculated on several occasions, to use as an index of dilution by meltwater.
Mathematically,

$$V_m = \frac{V_s Na_s}{Na_m} \tag{1}$$

where V_m and V_s are the flow volumes at the mouth of the stream and sewage outfall, respectively, and Na_m and Na_s are the concentrations of sodium. It is assumed that the concentration of sodium in meltwater is insignificant, that sodium retention in the stream is negligible, and that the volume of sewage discharged at the outfall is the same as the volume of water pumped from Strip Lake, which assumptions are correct for all practical purposes (Schindler et al. 1974). This procedure can be expected to give only approximate values, because thawing and refreezing of sewage below the outfall cause its nutrient content to be heterogeneous (D. W. Schindler unpublished data).

PHYTOPLANKTON

Phytoplankton samples were taken at several depths in connection with productivity studies. These were preserved in acid-Lugol's solution until counted by the Utermöhl (1958) technique.

SEDIMENT INTERSTITIAL WATER

A 1.5-m sediment core was taken at a depth of 8.5 m on August 16, 1970, using a mini-Mackereth corer. Processing of the core and chemical analysis of interstitial waters were as described by Schindler et al. (1974). Major reactive minerals were determined by X-ray diffraction. Methods were similar to those used by Brunskill et al. (1971).

NUTRIENT ADDITION EXPERIMENTS IN TUBES

To confirm that the response of Meretta Lake to increased nutrient loading was typical for lakes of the area, four closed polyethylene cylinders, 10 m long and 0.25 m in diameter, were installed in Char Lake on July 3, 1972. Cylinders were suspended under the lower ice surface, where they received natural light conditions. Once a week for 5 wk each cylinder was pulled to the surface, opened, and an integrated water sample was taken with a 10-m length of tygon tubing. After the weekly sampling, nutrient solutions were added according to the following scheme:

cylinder	addition
1	no enrichment
2	PO_4–P, 5 μg/liter
3	NO_3–N, 75 μg/liter
4	PO_4–P, 5 μg/liter; and NO_3–N, 75 μg/liter

Nutrients were dispersed uniformly in the cylinders by mixing them with a volume of water which would just fill the tygon sampling tube, pouring this into the sampling tube while it was extended full depth into the cylinder, then pulling the sampling tube up slowly releasing the nutrient uniformly throughout the length of the polyethylene cylinder. After sampling and fertilization, cylinders were pulled back beneath the ice. An aliquot of the water was filtered for chlorophyll analysis as described by Kalff et al. 1972. On days 0, 14, and 28, samples were also preserved for phytoplankton counts and identification.

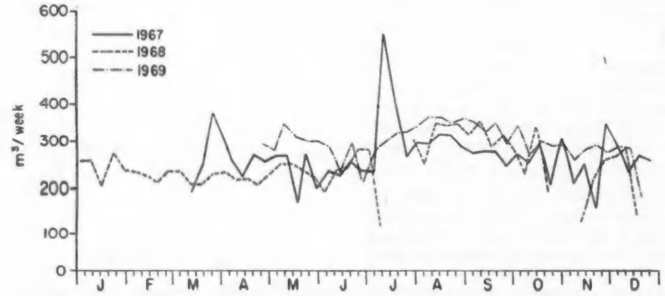


FIG. 3. Water usage for the Resolute Bay airport, 1967–69.

Results

TEMPERATURE

The lake developed temperatures as high as 7 C during the ice-free period without stratifying (Fig. 4). Under ice, temperatures seldom exceeded 1 C. The annual thermal regime was otherwise similar to that described by Schindler et al. 1974 for Char Lake, although Meretta froze a few days before Char Lake at a slightly higher water temperature, and became free of ice a few days earlier. Maximum ice thickness, 2.35 m, was observed in 1971, when 54% of the water volume froze. Snow cover tended to be higher than Char Lake, averaging 10–20 cm, reducing light entering the lake to about 1% of surface solar radiation (H. E. Welch and J. Kalff unpublished data). The ice-free season was longest in 1971 (6 wk), and shortest in 1972, when ice never completely left the lake.

CHEMISTRY

Phosphorus and nitrogen entered the lake in great quantities from the sewage inflow during spring runoff in mid- to late May 1971. Total dissolved phosphorus concentrations in the lake rose from less than 10 to over 200 µg/liter for a short period (Fig. 5). Because most of this dissolved phosphorus was molybdate-reactive (Fig. 5b), much of it was probably in a suitable form for stimulating plant growth. This is confirmed by the nearly total depletion of dissolved phosphorus during July, along with rapid increases in particulate phosphorus (Fig. 5c). Phosphorus concentrations decreased throughout the winter. When corrected for freeze-out, data showed that 46% of the phosphorus in the lake in September disappeared in about 250 days (Table 1).

Most of the dissolved nitrogen entered the lake as ammonia (Fig. 6a and b). As found for phosphorus, this disappeared rapidly during July. Nitrate nitrogen, which was low in sewage, reached maximum concentrations before sewage entered the lake during spring melt. This too disappeared quickly after spring melt flow decreased (Fig. 6c). Increases in particulate nitrogen corresponded with decreases in dissolved forms (Fig. 6d). As for phosphorus, there was a net flux of nitrogen into sediments throughout the winter (Table 1).

As for nitrate, bicarbonate concentrations were highest just before the spring sewage runoff began. When phosphorus and nitrogen began to flow into

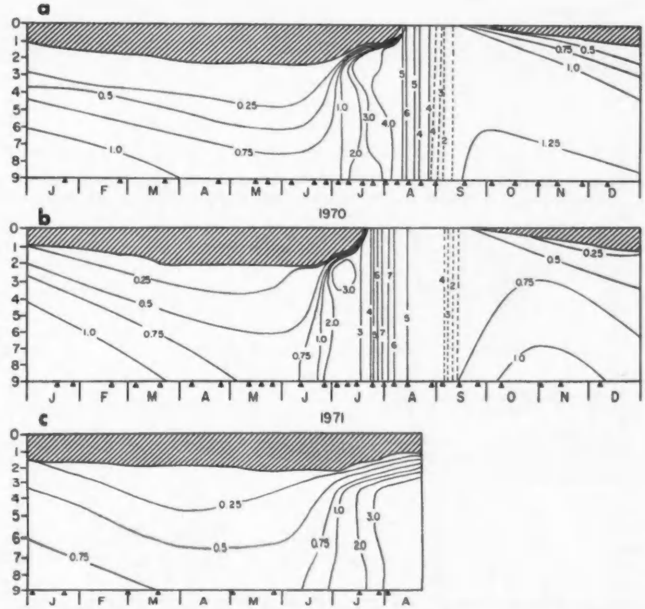


FIG. 4. Temperature isopleths for Meretta Lake, 1970–72. Arrows at the bottom of panels designate sampling dates.

the lake, uptake of carbon by phytoplankton caused a substantial decrease in gaseous CO_2, which resulted in a substantial increase in pH of the lake during July (Fig. 7a–c). As expected, sestonic carbon had a seasonal pattern similar to sestonic N and P (Fig. 7d). When total carbon values are considered, however, it is obvious that there was considerable metabolic regeneration of the element from sediments during the winter (Table 1).

The annual silicate maximum, too, occurred before the onset of the sewage inflow. The increase in concentration during winter was far too high to be accounted for by freezing-out of ice. Approximately 4.8 mg/m^2 appeared to return from sediments. Like nitrate and carbon, it was rapidly depleted by phytoplankton (Fig. 8) in the early spring. Values for conductivity and major ions during late winter were over twice those observed in summer (Fig. 9 and 10). Once again, there was evidence for significant return from sediments (Table 1).

Sulfate was the sole exception among major ions, with considerable decreases evident over winter (Table 1). However, because sulfide was not measured, sulfate data cannot be corrected for reduction to sulfide, and the flux of sulfur between water and sediments cannot be estimated.

Total dissolved iron remained low throughout the year, only reaching 5 μg/liter in bottom waters in late winter.

Oxygen was never totally depleted, reaching an average concentration of 4 mg/liter by late May (Fig. 11). Without the concentration by freeze-out, values would have been much lower. High values were observed under ice in June and early July as the result of high phytoplankton production.

PHYTOPLANKTON

Phytoplankton standing crops, as measured by chlorophyll *a*, began to increase under the ice after mid-March, probably in response to rapidly increasing light. Rapid increases occurred in June and July, when runoff was entering the lake (Fig. 12, see also Kalff et al. 1972). Rather large standing crops remained throughout the early fall, but these declined rapidly during winter darkness.

Peridineae (chiefly *Gymnodinium* and *Peridinum*) were important during the spring and summer of 1969, 1970, and 1971. During the summer months of 1969, heterotrophic flagellates, *Ochromonas*,

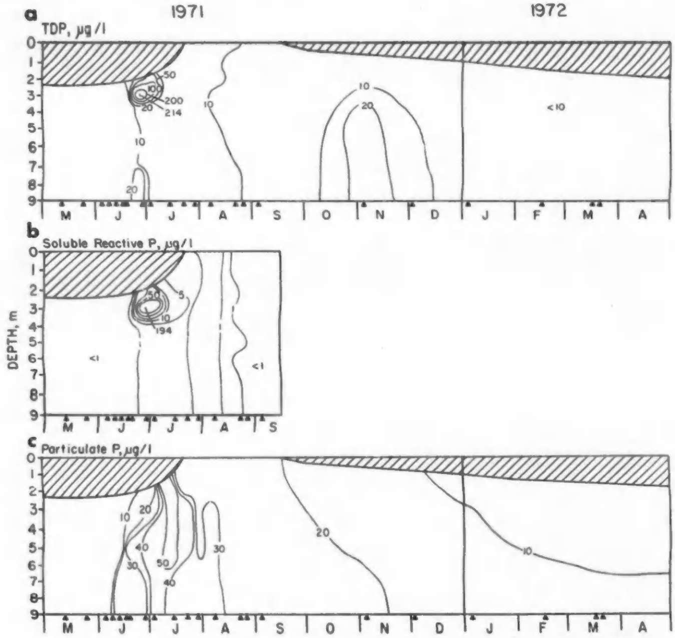


FIG. 5. Concentrations of total dissolved phosphorus (TDP), soluble reactive phosphorus (SRP), and particulate phosphorus (PP) in Meretta Lake, 1971–72.

TABLE 1. Regeneration of several elements from the sediments of Meretta Lake during the winter of 1971–72 (data from September 3–May 10). All values are corrected for freeze-out. A(+) indicates net movement of a given element from sediments into water, and a (-) indicates net movement from water to sediments.

	Mass in lake on Sept. 3 (*metric tons*)	Mass in lake after 250 days (*metric tons*)[a]	Total change over winter (%)	r^2[d]	Sediment–water exchange (*mg/m²/day*)	95% CL[e]
Total P	0.029	0.0068	-76	0.76	-0.34	±0.23
Total N	0.444	0.242	-45	0.26	-3.08	±2.82
Total C	14.4	23.9	+66	0.96	+145.0	±68.3
Ca^{+2}	16.7	22.1	+33	0.98	+82.4	±9.5
Mg^{+2}	6.2	7.6	+23	0.75	+21.4	±12.3
Na^{+}	9.0	11.0	+22	0.72	+30.5	±19.1
K^{+}	0.55	0.72	+31	0.81	+2.60	±1.25
Cl^{-}	16.4	17.7	+20	0.49	+19.8	±18.4
SO_4^{-2} c	4.6	3.2	-30	0.58	-21.4	±20.5
Si	0.021	0.336	+1500	0.64	+4.81	±3.62
Cond., weighted mean[b]	181	219	+21	0.74	-	

[a] Calculated from regression equation.

[b] $\bar{c} = \int_{z=0}^{z=z_m} (c_z d_z)/V$ where $\bar{c}$ is the weighted mean conductivity, c_z is the conductivity at depth z and V is the volume of the lake.

[c] Uncorrected for H_2S formation.

[d] All r^2 values are significant at the 95% level.

[e] CL, confidence limits.

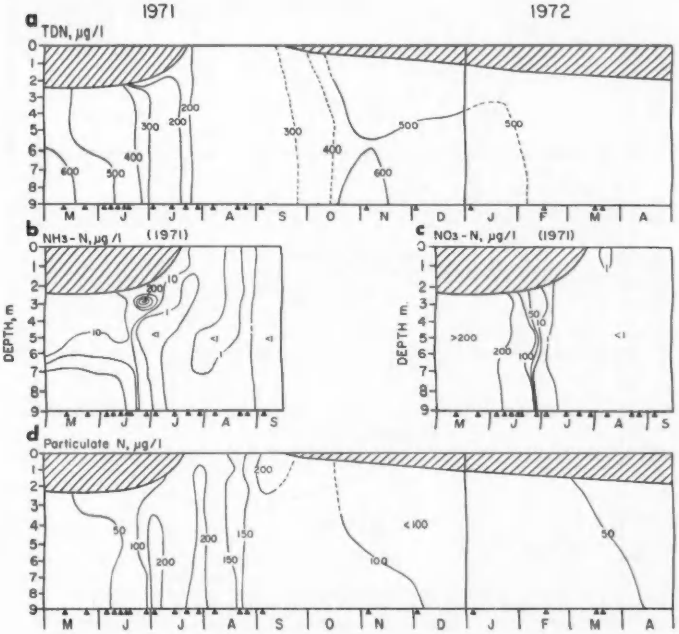


FIG. 6. Concentrations of total dissolved nitrogen (TDN), ammonia, nitrate, and particulate nitrogen (PN) in Meretta Lake, 1971–72.

Dinobryon, *Ankistrodesmus*, and *Chlorella* were important. In 1970 these genera were replaced by *Chlamydomonas* in July, *Anabaena* in August, and *Cyclotella glomerata* in October. The last-named species was still important in December of 1970, whereas *Ochromonas*, *Dinobryon*, and heterotrophic flagellates had been important in 1969.

Phytoplankton biomass and chlorophyll in Meretta Lake were far higher than in nearby Char Lake (H. Kling unpublished data). The maximum biomass recorded in Meretta was 16,000 mg/m^3 at a depth of 5 m in 1969 (chiefly Peridineae), and 14,400 mg/m^3 at a depth of 5 m in the summer of 1970 (chiefly Peridineae plus Chlorophyta); the mean phytoplankton biomass was approximately 8500 mg/m^3 for the summer months of 1969, and 5500 mg/m^3 for the summer of 1970.[4] Summer maxima in Char Lake were 550 and 200 mg/m^3 in the same 2 yr. Likewise, summer chlorophyll concentrations in Meretta Lake were 3–5 mg/m^3 compared to 0.13–0.69 mg/m^3 in Char Lake (Kalff et al. 1972). Fewer samples were taken in 1971, but seasonal dynamics appeared to be similar.

Winter minimum biomass in Meretta Lake was about 125 mg/m^3 in all years. The minimum value occurred in January of 1969–70 and in February of 1970–71. Dominant phytoplankters were small blue-greens and small chrysophyceans.

---

[4] Biomass values are "live" biomass calculated by measuring the dimensions of cells, calculating an approximate volume, and assuming a density of 1.00.

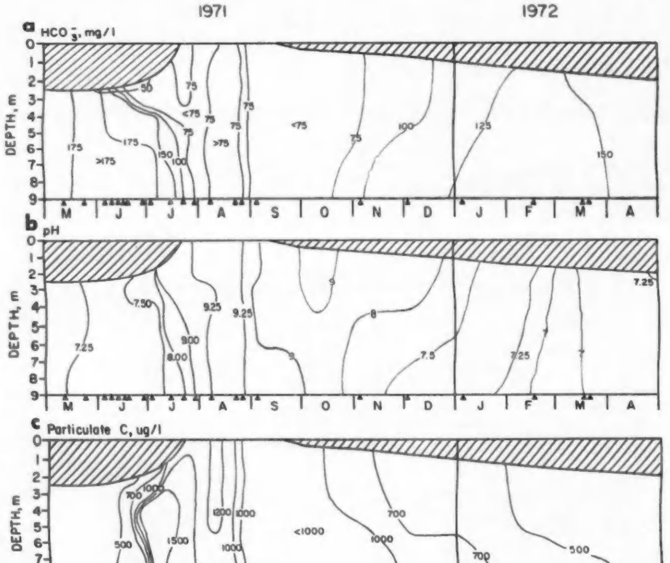


FIG. 7a–d. Bicarbonate, pH, particulate carbon (PC), and P_{CO_2} in Meretta Lake, 1971–72.

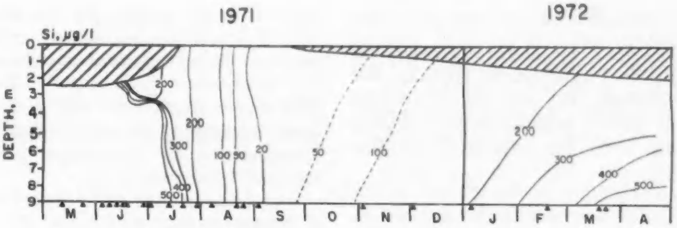


FIG. 8. Soluble reactive silicate (Si) in Meretta Lake, 1971–72.

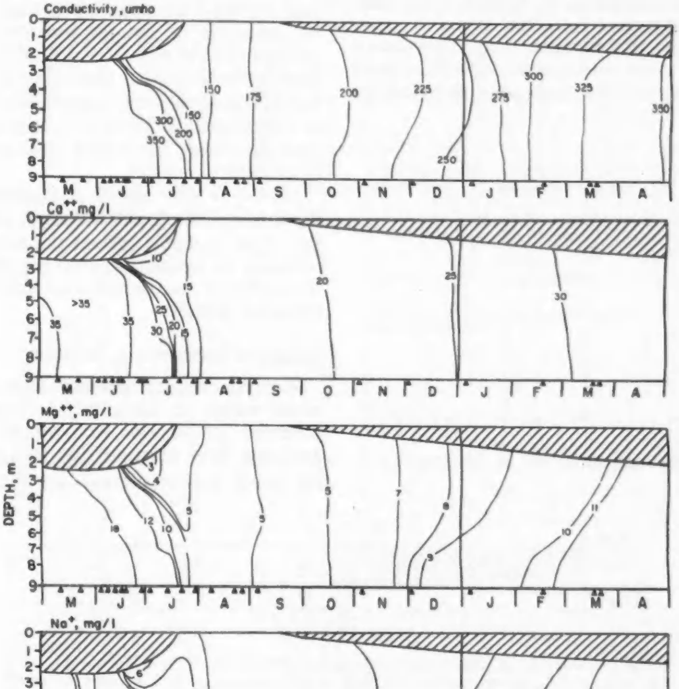


FIG. 9. Conductivity and major cations in Meretta Lake, 1971–72.

NUTRIENT INPUT FROM SEWAGE

Sewage from the airport was higher in phosphorus than would be expected at temperate latitudes, but about equal in nitrogen. The N:P ratio averaged only 1.63, where typical values are 4–5 (Weibel 1969; Vollenweider 1968). The average Na:P ratio was 11.5:1.

The concentration of Na at the stream mouth was only 10–60% of that leaving the sewage outfall, indicating 2–10× dilution by unpolluted meltwater. A rough seasonal trend was evident (Fig. 13), with highest concentrations in August, after most of the snow had melted from the basin.

Concentrations of nitrogen and phosphorus decreased more than could be accounted for from the dilution rate of Na, indicating considerable removal in the stream. Na was diluted an average of 3.1 times between sewage outfall and stream mouth; ΣP was apparently diluted by 13.9 and ΣN by 13.1 times. This indicates that approximately 78% of the phosphorus and 76% of the nitrogen were removed by the stream and its biota, if it is assumed that an insignificant amount of Na is removed by the biota.

Equation (1) gives an estimated annual discharge at the stream mouth of 33,000 m^3, with an average ΣP concentration of 1500 mg/m^3. This would represent an input of 0.19 gP/m^2 of lake surface per year to the lake from the sewage effluent. Based on chemistry of natural streams in the area, an additional input of 0.05–0.1 g/m^2 could be expected from natural sources (Schindler et al. 1974). The equivalent figures for nitrogen are an average ΣN of 2500 mg/m^3, an input of 0.32 g/m^2 per year from sewage, and an input of 0.23–0.46 g/m^2 per year from natural sources.

Figure 13 also shows a seasonal trend in the P:Na ratio, with lowest values in mid- to late summer. This probably reflects the higher retention of nutrients by stream biota during the warm part of the summer, as the standing crop in the stream increased greatly.

SEDIMENT INTERSTITIAL WATERS

A steep chemical gradient from sediment interstitial waters to the overlying water column was observed for all ions analyzed (Table 2). Larger gradients were observed for K and Ca, elements for which greater sedimentary return was found.

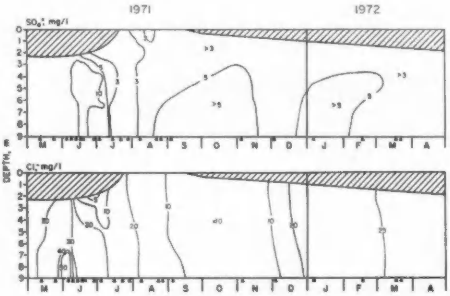


FIG. 10. Sulphate and chloride in Meretta Lake. 1971–72.

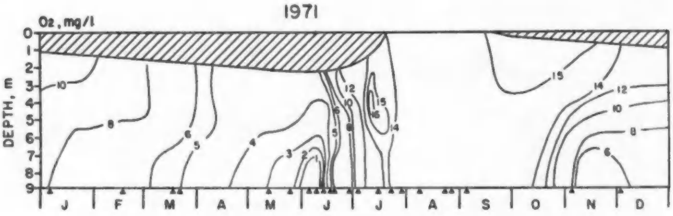


FIG. 11. Oxygen concentration in Meretta Lake, 1971.

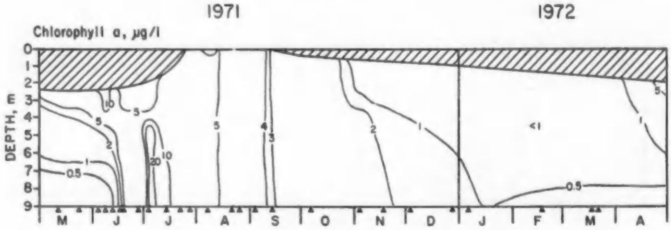


FIG. 12. Chlorophyll *a* concentration in Meretta Lake, 1971–72.

TUBE EXPERIMENTS

Phytoplankton biomass and chlorophyll increased dramatically in the bag receiving phosphate plus nitrate (Fig. 14 and 15). The bag receiving only phosphorus showed significant increases in phytoplankton, but not in chlorophyll. In contrast, the control bag and the bag receiving only nitrate showed little or no increase in standing crop.

The increase in standing crop in P and P+N bags was due largely to Peridineae, which displaced Chrysophyceae (Fig. 14).

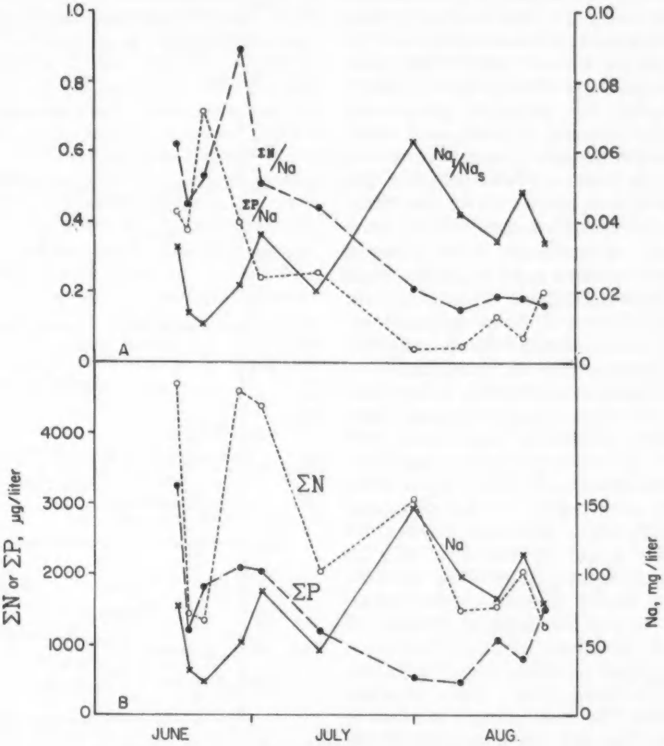


FIG. 13. A, The ratio of Na concentration at the mouth of the sewage inflow (Na_I) stream to that in sewage (Na_s); also the ratios (by weight) of ΣN and ΣP to Na at the mouth of the inflow stream. B, Concentrations of ΣP, ΣN, and Na at the mouth of the sewage inflow stream.

TABLE 2. Chemical constituents of Meretta Lake water, 1971–72 and sediment interstitial waters, August 16, 1970.

Depth in core (*cm*)	Conductivity (*μmho/cm*) (*25 C*)	mg/liter				
		Ca	Mg	Na	K	Cl
lake water (annual range)	150–350	10–35	5–18	<8–20	<0.5–1.5	<10–50
0–20	1100	131	59	15	52	70
55–75	1375	182	82	11	7.0	26
110–130	1550	193	85	7.4	14	26

Discussion

It is puzzling that a steady state, in which as much nutrient reaches the lake as flows into the stream with sewage, does not appear to have developed. It may be that sedimentation of organisms in the pools along the stream accounts for this removal in much the same way as nutrient is removed by a lake (Schindler et al. 1973), or that the nutrient seeps down and freezes in a concentrated layer on permafrost around the streambed (Schindler et al. 1974). Agronomists have found that terrestrial soils have an extremely high affinity for phosphorus, which binds to clay minerals, so that loss of terrestrial phosphorus fertilizers is low, even after decades of application (MacLean and MacDonald 1973). Denitrification by stream biota is also a possibility. Further research is required to clarify this point.

The significance of sediments in the annual chemical regime of Meretta Lake is an interesting contrast to nearby, oligotrophic Char Lake. The sediments of both lakes have similar mineral compositions, chiefly calcite, dolomite, and aragonite. The Meretta sediments, however, contribute substantially to the chemical composition of the overlying water for all elements except nitrogen, phosphorus, and sulfur, whereas in Char Lake, only silica is supplied by sediments to any significant degree. The sewage input to Meretta Lake is therefore undoubtedly responsible for the difference. It was considerably higher than lake water in all constituents (Table 2 and 3). The effect may be caused by biological uptake, followed by sedimentation and release of the elements on decomposition, or it may be due to increased solution of sediment minerals caused by increased concentrations of organic acids resulting from the higher productivities and decomposition rates expected in a eutrophic lake. The lower oxygen tensions in Meretta than in Char did not appear to be responsible, because fluxes of elements early in winter when oxygen concentrations were high were identical to those in late winter under near anoxic conditions (Fig. 16).

The fact that neither phosphorus nor nitrogen returned from sediments, in spite of high influxes of the elements from sewage and low oxygen concentrations, is of particular significance to eutrophication, indicating that the lake would return quickly to natural conditions once the input of sewage ceased. Schindler et al. (1974) reached similar conclusions for the Precambrian Shield lakes of northwestern Ontario.

Standing crops of phytoplankton in Meretta Lake are lower than would be expected at temperate latitudes for similar high inputs of phosphorus in a lake of equal size. According to standing crop, the lake would be classified as mesotrophic by temperate standards (Sakamoto 1966; Winberg

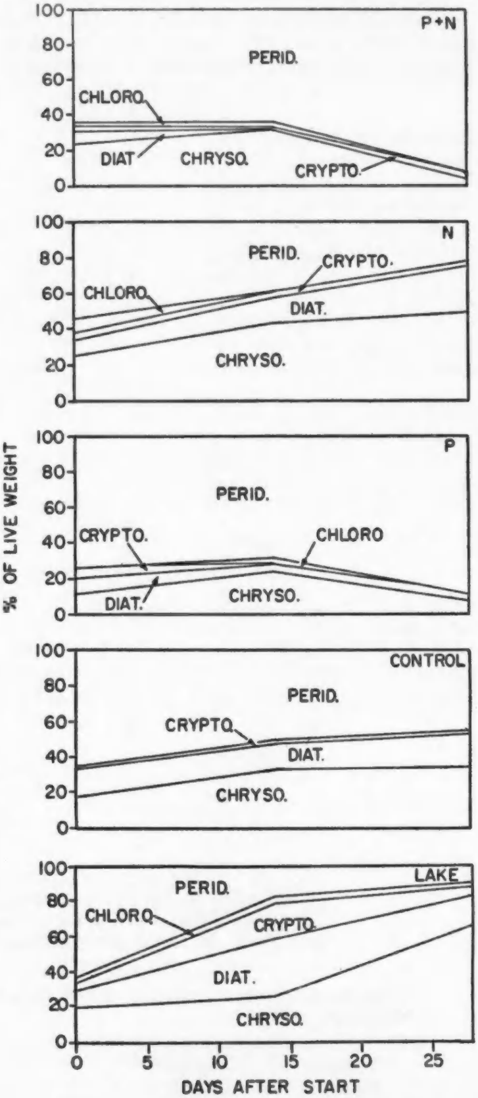


FIG. 14. Percentage composition of phytoplankton in Char Lake tube fertilization experiments, July 3–31, 1972. All nitrogen additions were 75 μg NO_3–N/liter per wk, and all phosphorus additions were 5 μg PO_4–P/liter per wk. Increases in biomass during the 4-wk period were: P+N, 2700%; N, −10%; P, 700%; control, 92%; lake, 17%.

1963; Vollenweider 1968), and nutrient inputs would normally create eutrophic conditions at temperate latitudes. Similarly, bacterial numbers and activity indicate that the lake is mesotrophic (Morgan and Kalff 1972). This difference may be due to a deficiency of nitrogen in Meretta Lake, after standing crops had increased by an order of magnitude, rather than latitudinal difference. Such deficiencies are common in sewage-enriched lakes of the temperate zone, where ratios of nitrogen to phosphorus in inputs are far lower than required for balanced algal nutrition. This prevents one from concluding that smaller blooms develop in relation to a given phosphorus loading in the arctic, because the greater blooms might develop if these elements were as abundant as in most temperate waters. On the other hand, they could also be the result of low input of solar radiation, which is 8×10^5 kcal/m^2 per year in Resolute, compared to $12–16 \times 10^5$ kcal/m^2 per year for most parts of the U.S. and southern Canada. This radiation is, of course, reduced even further by the ice and snow cover on arctic lakes (see Brylinski and Mann 1973).

Standing crops of phytoplankton were, however, 10–100 times higher than in nearby Char Lake, which does not receive significant cultural inputs of nutrients. This was particularly true for the summer season, when sewage was entering Meretta Lake. For example, comparing data for Char Lake in June–August of 1969–71 and Meretta Lake in 1969–70, Char Lake phytoplankton averaged about 125 mg/m^3, whereas in Meretta Lake they averaged about 4000 mg/m^3.

Differences in species composition were also noticeable. *Anabaena* and *Chlamydomonas* were present in Meretta, but not in Char. Peridineae were also far more important in Meretta during the spring and early summer, replacing the chrysophyceans and cryptophyceans present in unpolluted lakes of the area during the period. The overall phytoplankton assemblage in Meretta Lake was much different from that expected in a similarly polluted lake at temperate latitudes, where water blooms of green or blue-green algae would usually dominate the phytoplankton in mid- to late summer.

Occasional observations on North and Small lakes near Resolute confirmed that Char Lake

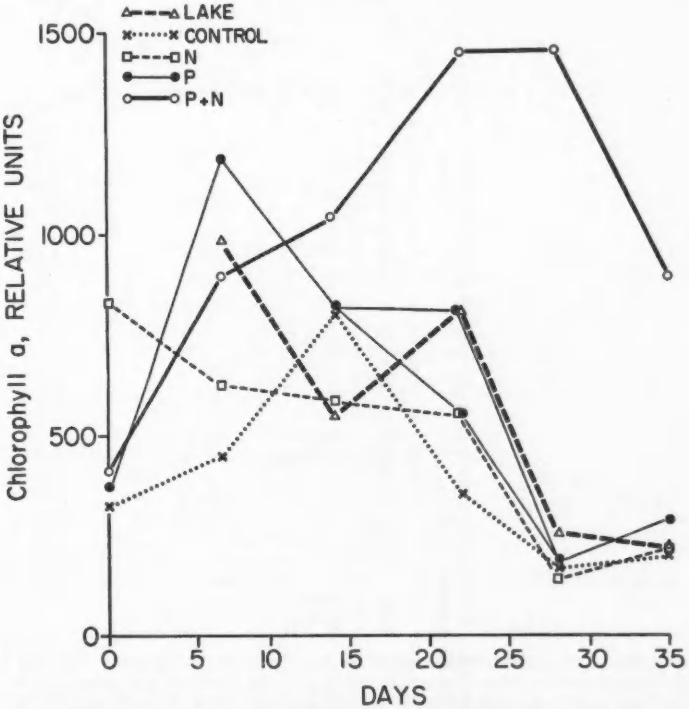


FIG. 15. Chlorophyll *a* concentrations in Char Lake tube fertilization experiments, 1972.

TABLE 3. Average composition of sewage from Resolute North Base. Values are averages of eleven 24-h composite samples taken from May 1971–April 1972. All values in mg/liter.

	TDP	Susp. P	NH_3–N	NO_3–N	TDN	Susp. N	HCO_3	Susp. C	Si	Ca	Mg	Na	K	Cl	SO_4	pH
Max	31.5	7.6	87.8	<0.007	121.3	12.8	806	7300	22.5	122	34	684	29	774	125	8.8
Min	5.6	0.3	0.2	<0.007	5.2	0.1	348	0	3.0	30	8	2	9	118	0	7.1
$\bar{x}$	12.5	2.2	33.3	<0.007	68.5	6.0	516	1300	7.0	70	20	208	15	342	57	7.4

phytoplankton biomass and species composition are typical for natural lakes of the region. This, plus the fact that nutrient-enriched bags in Char Lake responded by increases in standing crop, and changes to Peridineae, as observed in Meretta Lake, indicates that the response of Meretta phytoplankton, forming algal blooms in response to sewage, is not atypical for the area. The fact that blooms in bags appeared to require P to initiate a response, even though largest responses were obtained with P and N, indicates that as in most temperate lakes, phosphorus control is the key to eutrophication control in the Resolute area (Vollenweider 1968).

Excessive inputs of nutrients are known to increase productivity and result in a higher winter respiration rate. This can have severe effects on the biota of high arctic lakes because of the long period of ice cover and low light. Species in high arctic lakes are generally intolerant of low oxygen tensions and when such species are eliminated by anoxic conditions, there may be no species available to take over the vacant niche as there are in temperate lakes. For example, *Limnocalanus macrurus* was abundant in Meretta Lake until 1969. Eggs were laid as usual that winter but failed to hatch, and eggs retrieved from the bottom during spring 1970 had growths on them and did not hatch when placed in oxygenated water (Roff and Carter 1972; J. C. Roff personal communication). The animal has not reappeared and no other macroscopic

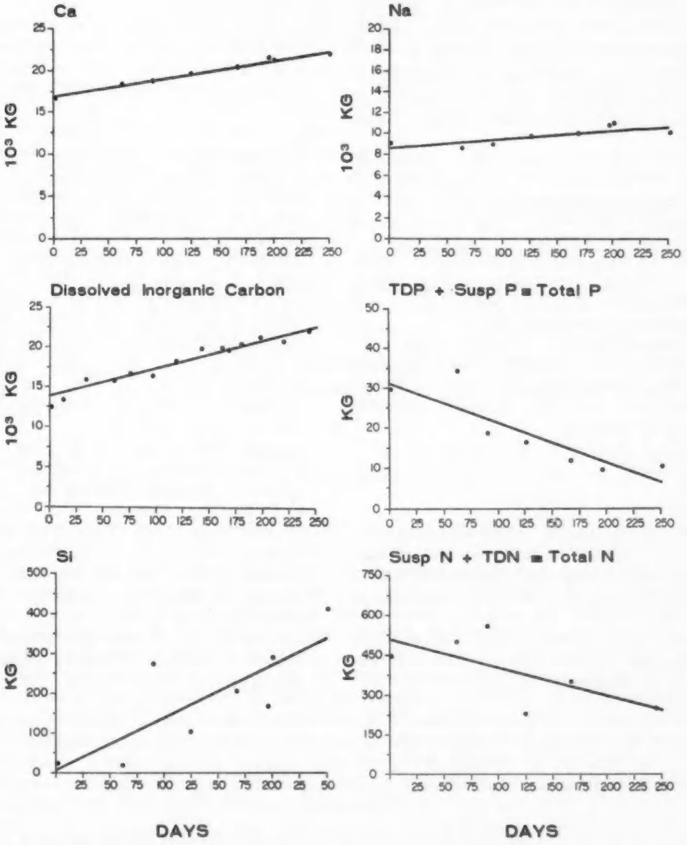


FIG. 16. Change in mass of several representative elements in Meretta Lake during the winter of 1971–72. Data used were collected from September 3, 1971 to May 10, 1972. All data are corrected for freezeout from ice. The regression lines shown were used to calculate the fluxes in Table 1.

zooplankter has replaced it, although a few cyclopoid copepods are occasionally found in the plankton. The Arctic char (*Salvelinus alpinus*) may also be experiencing difficulties. Only one young-of-the-year was found during the summers of 1971 and 1972, unlike previous years (W. MacCallum personal communication), suggesting that the eggs and/or fry, which overwinter on the bottom, are dying because of altered oxygen, food, or sediment conditions.

When large settlements are built during the current northern exploration and development "boom," the eutrophication problem cannot be ignored. Although large volumes of untreated effluent can cause problems similar to those at southern latitudes, it is also likely that properly treated and controlled effluents could be used to advantage in enhancing fish production through the simplified arctic food chain, providing care is taken not to cause excessive oxygen depletion under winter ice. Controlled experiments to evaluate such possibilities should be made now, before human settlements in the arctic pose a severe threat to natural waters.

Acknowledgments

Special thanks are due to Dr F. H. Rigler for his help and advice throughout the study and the preparation of the manuscript. V.E. Frost and P. Cross did many of the data calculations and plots.

This paper is contribution No. 21 of the Char Lake Project and contribution No. 250 of the Canadian Committee for the International Biological Program. The research was supported by C.C.I.B.P. and the Fisheries and Marine Service.

BRUNSKILL, G. J., D. POVOLEDO, B. W. GRAHAM, AND M. P. STAINTON. 1971. Chemistry of surface sediments of sixteen lakes in the Experimental Lakes Area, northwestern Ontario. J. Fish. Res. Board Can. 28: 277–294.

BRYLINSKI, M., AND K. H. MANN. 1973. An analysis of factors governing productivity in lakes and reservoirs. Limnol. Oceanogr. 18: 1–14.

KALFF, J., H. E. WELCH, AND S. K. HOLMGREN. 1972. Pigment cycles in two high Arctic Canadian lakes. Verh. Int. Ver. Limnol. 18: 250–256.

MACLEAN, A. J., AND E. M. MACDONALD. 1973. Agricultural contributions to nutrient enrichment of waters in watersheds of Lake Erie, Lake Ontario and the international section of the St. Lawrence River. Rep. to Can. Dep. Agr. Task Force in Support of International Joint Commission. 107 p.

MASEMAN, V. 1971. Phosphorus budget of an Arctic lake. M.Sc. Thesis. Univ. Toronto, Toronto, Ont. 56 p. + appendices.

MORGAN, K. C., AND J. KALFF. 1972. Bacterial dynamics in two high Arctic lakes. Freshwater Biol. 2: 217–228.

ROFF, J. C., AND J. C. H. CARTER. 1972. Life cycles and seasonal abundance of the copepod *Limnocalanus macrurus* Sars in a high Arctic lake. Limnol. Oceanogr. 17: 363–370.

SAKAMOTO, M. 1966. The chlorophyll amount in the euphotic zone of some Japanese lakes and its significance in the photosynthetic production of phytoplankton community. Bot. Mag. (Tokyo) 79: 77–88.

SCHINDLER, D. W., H. KLING, R. V. SCHMIDT, J. PROKOPOWICH, V. E. FROST, R. A. REID, AND M. CAPEL. 1973. Eutrophication of lake 227, Experimental Lakes Area, northwestern Ontario by addition of phosphate and nitrate: the second, third, and fourth years of enrichment, 1970, 1971, and 1972. J. Fish. Res. Board Can. 30: 1415–1440.

SCHINDLER, D. W., H. E. WELCH, J. KALFF, G. J. BRUNSKILL, AND N. KRITSCH. 1974. Physical and chemical limnology of Char Lake, Cornwallis Island (75°N lat.). J. Fish. Res. Board Can. 31: 585–607.

UTERMÖHL, H. 1958. Zur Vervollkommung der quantitätiven Phytoplanktonmethodik. Mitt. Int. Ver. Limnol. 9: 1–38.

VOLLENWEIDER, R. A. 1968. The scientific basis of lake and stream eutrophication, with particular reference to phosphorus and nitrogen as eutrophication factors. Organ. Econ. Coop. Dev. Paris (DAS/CSI/68) Tech. Rep. 27: 1–182.

WEIBEL, S. R. 1969. Urban drainage as a factor in eutrophication, p. 383–403. *In* Eutrophication: causes, consequences, correctives. Natl. Acad. Sci. Washington, D.C.

WINBERG, G. G. 1963. The primary production of bodies of water. USAEC Transl. AEC-tr-5692: 601 p.

The Morphoedaphic Index, a Fish Yield Estimator — Review and Evaluation[1,2]

R. A. RYDER

Ministry of Natural Resources
Fish and Wildlife Research Branch, Thunder Bay, Ont.

S. R. KERR

Ministry of Natural Resources
Fish and Wildlife Research Branch, Maple, Ont.

K. H. LOFTUS

Ministry of Natural Resources
Sport Fisheries Branch, Toronto, Ont.

AND H. A. REGIER

Ramsey Wright Laboratories
University of Toronto, Toronto, Ont.

RYDER, R. A., S. R. KERR, K. H. LOFTUS, AND H. A. REGIER. 1974. The morphoedaphic index, a fish yield estimator — review and evaluation. J. Fish. Res. Board Can. 31: 663–688.

The morphoedaphic index (MEI), a fish yield estimator, was historically reviewed and evaluated. Background papers leading to the development of the MEI were discussed, as well as more recent advances. The MEI was defined and its criteria for use examined. The significance of its components — total dissolved solids and mean depth — were explained. The MEI was compared with related models developed by other workers. The global range of the MEI was outlined as well as restrictions on its use. Sustained fish yields at different MEI values for various climatic regions were predicted. Several special applications of the MEI were described, including: prediction of angling yield in north-temperate lakes; prediction of commercial fish yield on a newly created reservoir; indicator of ecological stresses and changing environments; and contrasting responses to cultural eutrophication in the littoral and profundal zones of lakes. The implications of the MEI for ecological theory were explored, and its potential for future application in management was outlined.

RYDER, R. A., S. R. KERR, K. H. LOFTUS, AND H. A. REGIER. 1974. The morphoedaphic index, a fish yield estimator — review and evaluation. J. Fish. Res. Board Can. 31: 663–688.

Les auteurs présentent une revue historique et une évaluation de l'indice morphoédaphique (IME), un estimateur du rendement en poisson. Ils examinent les articles de base qui ont amené le développement de l'IME, de même que les travaux récents. Ils définissent l'IME et examinent les critères de son emploi. Ils expliquent la signification de ses composants, solides totaux dissous et profondeur moyenne. Ils comparent l'IME avec les modèles apparentés développés par d'autres chercheurs. Ils donnent, dans ses grandes lignes, la gamme globale de l'IME, de même que les restrictions dans son usage. Ils prédisent les rendements en poisson, sur base soutenue, à diverses valeur d'IME et pour diverses régions climatiques. Ils décrivent plusieurs applications spéciales de l'IME, y compris: prédiction du rendement commercial en poisson dans un réservoir nouvellement formé; indicateur de contraintes écologiques et d'environnements changeants; et réponses contrastantes à l'eutrophisation agricole dans les zones littorales et profondes des lacs. Ils explorent les implications de l'IME à l'endroit de la théorie écologique et esquissent son potentiel pour application future à l'aménagement.

Accepted December 31, 1973

[1,2]Footnote see page 664

Printed in Canada (J3262)

THE morphoedaphic index (Ryder 1964a; 1965) is an empirically-derived formula that was described initially as a convenient method of rapidly calculating potential fish yields from unexploited north-temperate lakes. Since its inception, the constraints on the use of the morphoedaphic index (MEI) have been relaxed as it has been applied to sets of lakes other than those for which it was originally devised. Various investigators have clarified our understanding of the MEI (e.g. Jenkins 1967; Regier et al. 1971; and Henderson et al. 1973) and have extended the application of this index to other climatic systems.

Scientific and practical aspects of the MEI have been discussed in some depth at three recent international symposia, i.e. "The Second Seminar on Fish Stock Assessment" at Bujumbura, Burundi, in June 1971 (Regier 1971), "Salmonid Communities in Oligotrophic Lakes" held at Geneva Park, Canada in July 1971 (Loftus and Regier 1972), and the "Technical Conference of Fishery Management and Development" at Vancouver, Canada, 1973 (Ricker and Weeks 1973). Recently, the MEI has found its way into a text book on ecology (Watt 1973) in which it was used as an example of energy flow rate through biological systems depending on resource availability.

The scientific approach implicit in the MEI is basically complementary to that of dynamic functional modelling of ecosystems (Walters 1971), which has enjoyed the spotlight in recent years. The MEI is essentially an index at the ecosystem level of organization derived from statistical analyses of a large number of ecosystems. These two approaches traditionally complement each other in science — a point often overlooked by the more enthusiastic functional modellers or ecological reductionists of recent years (Regier 1973).

In this paper we review the MEI's original description, history of development, advances by other workers, criteria for application, and inherent ecological significance. It is hoped that this historical treatment of a simple index (MEI and related indices) will encourage others to take the next step, which is to develop a more comprehensive model in which climatic variables are included, thereby integrating all the models for the various climatic regions of the world.

The morphoedaphic index defined is a function of an edaphic variable and a morphological variable (in this case morphometric) both defined with respect to the entire aquatic ecosystem. Specifically, in its simplest form it is the ratio of total dissolved solids (Am. Publ. Health Assoc. 1960) and mean depth of the water body (Hutchinson 1957). As first used in Canada, it was found to be proportional to the long-term fish yields of a series of lakes in a region that was moderately homogeneous with respect to climate, social incentives on intensity of exploitation, and general nature of the ionic composition of the dissolved materials.

The term "morphoedaphic" was first conceived when its potential broad applicability suggested the need for a single term descriptive of its two components (Ryder 1964a; 1965). Morphoedaphic was derived from the Greek; i.e. "morph" = form, and "edaphos" = bottom. The adjectival form "morphoedaphic" retains the original connotation for "morph" but utilizes the contemporary meaning of edaphic to denote effects due to soil or topography rather than climate (Ryder 1965).

Contributory Research

Rounsefell (1946) found an inverse relation between fish yield and lake area, that is, large lakes produced less fish per unit area than small lakes. However, had Rounsefell access to other morphometric data from the same series of lakes, an even better relation would have been obtained by substituting mean depth for area. Large lakes *generally* are deeper than small lakes for any given bottom configuration (see Hayes 1957, figure 2). Hence the relation observed by Rounsefell was not primarily that of yield regressed on area, but rather that of yield on mean depth. Shallower and smaller lakes generally contain a larger proportion of the substrate in the euphotic zone and exhibit proportionately larger perimeter per unit water area (Larkin 1964), indicating the relative importance of the littoral zone to fish production. Conversely, large (and deeper) lakes may have most of their substrate in the aphotic zone and fish production therefore may depend for the most part on food webs originating in the littoral or pelagic zones. Perhaps for the reasons implied above, long-term yields per unit area are more closely related to mean depth than to area, both relations being inverse. This was recognized by Rawson (1952) who suggested that greater depth constrains fish production well beyond the limit where increase in area has any significant effect.

Carlander (1955) in a reanalysis of Rounsefell (1946) indicated that Rounsefell's regression of yield on area may actually have encompassed an

---

[1] This paper, part of a special issue that comprises a comprehensive review of Limnology in Canada, was prepared to mark the 19th Congress of the International Association of Limnology (SIL), in Winnipeg, Man., during August 1974.

[2] Contribution 73-15 — Ontario Ministry of Natural Resources, Maple, Ont.

inverse relation between fishing effort per unit area over a range of lakes of diverse areas. This observation substantiates that which is now generally accepted — small lakes are exploited more efficiently per unit surface area than large lakes when both are subjected to proportionally similar fishing effort.

Rawson (1951) described the usefulness of mineral content (total dissolved solids) as "a rough indicator of edaphic conditions which must in some measure affect the productivity of lakes." He suggested that a preoccupation with ionic components and limiting elements had led to neglect of the measurement of total dissolved solids as a simple and useful index to the conditions which lie behind productivity. Rawson qualified this observation by noting that differences in productivity in the Laurentian Great Lakes could not be ascribed to differences in mineral content alone. For example, lakes Erie and Ontario have approximately the same mineral content, but the former lake has a fish yield about 10 times that of the latter lake. This difference could be explained better on a morphometric basis rather than an edaphic one, as Lake Ontario has a mean depth about 5 times that of Lake Erie. Rawson (1951) suggested that the relative shallowness of Lake Erie (morphometry) far outweighed the effect of the mineral content or edaphic influence. On the other hand, the relatively great depths of Lake Ontario may be related to Lundbeck's (1934) secondary, or morphometric oligotrophy.

Let us consider this comparison further in these two Laurentian Great Lakes. Shallow Lake Erie has more shoal areas for the growth and attachment of photosynthetic organisms with a resulting greater biomass of grazing and (ultimately) predator species than Lake Ontario. A larger proportion of the water mass of Lake Erie is in the euphotic zone, allowing for relatively greater mixing and ultimately higher productive efficiency averaged over any water column of constant cross-sectional area. The shallower depths of Lake Erie have contributed to an overall warmer temperature regime, allowing for more rapid growth and consequently production, especially of the warm-water eurytherms. Additionally, the large area of profundal zone in Lake Ontario might serve as a "nutrient sink," a zone in which organic matter (and ultimately nutrients) accumulate and become unavailable to the system, at least for large parts of the year in which density stratification occurs.

A plot of fish yield on mean depth for the five Laurentian Great Lakes and eight large Canadian lakes for which long-term catch statistics were available resulted in a significant relation (Rawson 1952). A hyperbolic distribution on arithmetic axes suggested a double logarithmic transformation which resulted in a linear relation of predictive utility for large lakes; i.e. $\log (Y - 0.56) = 1.1677 - 0.7029 \log \bar{z}$, where Y is commercial fish yield per unit time and area and $\bar{z}$ is mean depth.[3]

The inflection of the fitted curve at about the 18-m mean depth level was suggested by Rawson to indicate the theoretical morphometric separation between shallow lakes with high yields (i.e. morphometrically eutrophic) from deep oligotrophic lakes with low yields. The empirically derived constant, 0.56, suggested that a lake of infinite depth would still produce a small crop of fish, i.e. about 0.5 kg/ha. This value for Rawson's set of North American north-temperate lakes represents a limnetic productivity measure in the sense that production is sustained by the plankton and plankton feeders in lake areas where benthos and bottom feeding fish form an insignificant portion of the total biomass (Rawson 1955).

Rawson (1952) considered the depth of a lake to be important mainly for its effects on temperature, thermal stratification, and the circulation and dilution of nutrient materials. He suggested that mean depth might be correlated with standing crops of both plankton and bottom fauna as well as with sustained fish yield. He provided data to support this hypothesis (Rawson 1955) in which biomass curves for both plankton and benthos regressed on mean depth showed an inverse hyperbolic relation similar to that for fish yield. The curve for benthos has recently been duplicated by Alley and Powers (1970) using some of Rawson's earlier data supplemented with more recent information.

Rawson (1955) indicated that the factors affecting lake productivity could be conveniently grouped into three broad categories, namely, edaphic, morphometric, and climatic. He proposed that multiple correlation analyses of these factors be executed as soon as suitable climatic and edaphic data became available.

Carlander (1955) found no correlation between standing crops of fishes (biomass per unit area) and areas of lakes. Biomass per unit area decreased, however, with an increase in maximum depth of trout lakes, warmwater lakes, and reservoirs; also significant increase of biomass occurred in these waters with an increase of carbonate content (methyl orange alkalinity). Moyle (1956) obtained close graphical correlations between carrying capacity of lakes for fish (biomass per unit area) and four independent variables, namely, total phosphorus, total nitrogen, total alkalinity, and salinity.

---

[3] We have revised Rawson's notation and terminology to conform with current practice. Hence fish production (p) becomes yield (Y) and mean depth (d) becomes ($\bar{z}$). The equation has also been transformed to metric units (see Rawson 1955).

Northcote and Larkin (1956) tested standing crops of plankton, benthos, and fish regressed on various abiotic variables, including total dissolved solids and mean depth for a series of British Columbia lakes. Individual relations among these variables were not found to be strong. However, a bio-index combining relative measures of plankton, bottom fauna, and fish abundance used in multiple regression analysis with total dissolved solids and mean depth as independent variables resulted in a significant relation. Mean depth, however, accounted for only a minor portion of the variability, suggesting that differences in this abiotic factor were important only in lakes with equivalent concentrations of total dissolved solids. Northcote and Larkin concluded that dissolved nutrients are a primary factor in determining levels of productivity. However, the failure of a narrow range of total dissolved solids to show a correlation with standing crops of organisms suggested the need for considering other abiotic variables, such as mean depth. It was suggested that only in the deepest and largest of lakes does mean depth appreciably deter production.

Satomi (1962) postulated that because alkalinity had a physiological effect on freshwater organisms and its concentrations fluctuated only slightly over a period of time, therefore it could be a useful indicator of freshwater fish yield. He found that catch was correlated with maximum depth and alkalinity for inland lake fisheries. Other correlations of lesser validity were alkalinity and fish harvest from rivers, and ichthyomass and alkalinity in pond culture. A negative correlation was evident between alkalinity and light penetration in eel pond culture, which was attributed to the copious addition of feed to the ponds.

Hayes and Anthony (1964) utilized a productivity index based on food chain length and standing crop or yield of fishes. This index was related to area, mean depth, and methyl orange alkalinity. The multiple regression analysis suggested that mean depth accounted for 29% of the total variation in the productivity index, area for 20%, and alkalinity for 18%. Unidentified residual factors constituted the remaining 33%. Unfortunately, mean depth and area, two of the abiotic variables, were correlated (Hayes 1957, figure 2), which tended to weaken any conclusions that might be drawn from this analysis.

History of Development

The morphoedaphic index (total dissolved solids divided by mean depth) was formulated by building on the previous work of other investigators, particularly Rawson (1951, 1952) and Northcote and Larkin (1956). Rawson's work, dealing with large lakes, pointed to the overwhelming influence of mean depth on fish yield, while Northcote and Larkin concluded that the edaphic factor was more important for the smaller British Columbia lakes. These considerations appear to be balanced within the MEI, where total dissolved solids exerted more influence in shallow lakes while mean depth was the dominant factor in deep lakes.

The MEI was first utilized on an empirical basis to estimate potential fish yield from a large number of unexploited lakes in northern Ontario (Ryder 1961). The index emerged from the results of rank correlation analyses and multiple regression analyses of the relation of fish yield to diverse abiotic variables. These included mean depth, total dissolved solids, total alkalinity, shore development factor, length of growing season, inorganic turbidity, latitude and altitude, July mean daily temperature, frost-free period, glacial history, transparency, mean temperature of the trophogenic zone, flushing rate, dissolved oxygen concentration in the hypolimnion, water level fluctuations, and various other factors. It was soon discovered that the rank correlation system imparted too much subjective judgment on the part of the investigator in defining category increments and weighting the variables proportionately.

Multiple regression techniques, while less subjective, introduced another difficulty, that of correlations within the set of independent variables. Many of the abiotic factors that were considered were at least partial correlates, which decreased the efficiency of the regressions. For example, total dissolved solids and total alkalinity were highly correlated (Ryder 1964); latitude and altitude were partially correlated with most of the climatic factors; mean temperature in the trophogenic zone was inversely correlated with dissolved oxygen concentrations in the hypolimnion and most morphometric factors considered were interrelated.

Three vital influences on productivity were recognized, namely, climate, geology of the watershed, and morphology of the lake basin. Only the climatic and edaphic factors were of first order significance and provided the essential sources of energy and nutrients. The morphometric factor may be considered a second order or mediating effect, as it serves mainly as a modifying factor of climate and geology by determining the character of the temperature and nutrient regimes, both seasonally and on shorter time scales (Regier and Henderson 1973). But although the morphometric effect is secondary, it may in extreme instances exert an influence of such large magnitude as to all but nullify the effects of favorable energy and nutrient inputs.

To reduce the complexity of the many morphometric, edaphic, and climatic abiotic variables to be considered in multiple regression, the climatic variable was held relatively constant by including only north-temperate lakes in the initial regression analyses (Ryder 1965). Yield regressed on mean depth resulted in a highly significant correlation coefficient (*r*) that could not be matched by any other single abiotic factor in the data set including total dissolved solids. Multiple regression with total dissolved solids as a second independent variable enhanced the relation further with fish yield, leaving a residual variance of only 25% to be explained, in the absence of marked climatic variability. Because the individual exponents were similar, the resulting multiple regression was simplified by taking the ratio of total dissolved solids to mean depth (the MEI) as a single independent variable and expressing the relation with yield in the form of a simple regression (Fig. 1). The ensuing equation $Y = 2.094X^{0.44610}$ (English Units, where $\bar{z}$ is in feet and yield in lb/acre per year) was further simplified to $Y \sim 2\sqrt{X}$ for ease of application in management. Here Y = fish yield; X = MEI.[4]

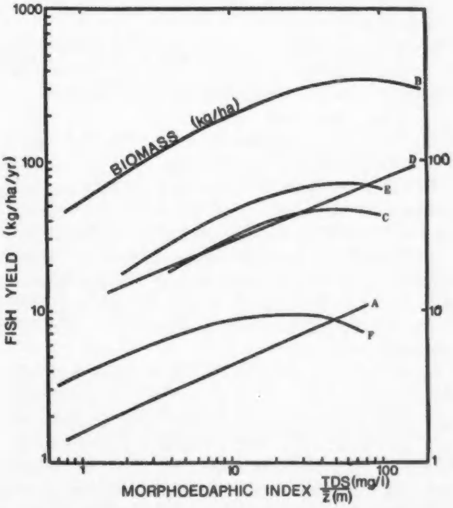


FIG. 1. Yield and/or biomass curves for four regional lake groups: A, yield curve for north-temperate lakes of North America (Ryder 1965); B, biomass curve for temperate and south-temperate reservoirs of the USA (Jenkins 1967); C, yield curve for Jenkins' reservoirs derived by Regier et al. (1971): D, yield curve for tropical African lakes using the models of Ryder (1965), and E, Jenkins (1967); F, yield curve of Finnish north-temperate lakes (J. Toivonen personal communication) using Jenkins (1967) model.

The next major advancement in our understanding of these interrelations was provided by Jenkins (1967). He approached the problem of biomass and yield estimates for 210 U.S. reservoirs by using multiple regression techniques with several abiotic variables. Four basic regressions involved (1) standing crop on the morphoedaphic index; (2) standing crop on total dissolved solids, shore development, and storage ratio; (3) sport fish harvest on total dissolved solids, growing season, age, area, and shore development; and (4) commerical harvest on growing season, mean depth, storage ratio, age, and water level fluctuation. Jenkins concluded that the most meaningful regression of predictive utility was that of standing crop on the morphoedaphic index (Fig. 1).

However, some notable differences were observed by Jenkins when he compared his regression of standing crop on the MEI with that of yield on MEI for north-temperate lakes (Ryder 1965). The latter regression for north-temperate lakes produced a higher correlation coefficient ($r = 0.856$; df = 22) than did Jenkins' work with U.S. reservoirs ($r = 0.325$; df = 108). Both were highly significant at the 1% level. The lower efficiency of the MEI with Jenkins' model may stem from the somewhat ambiguous characteristic of a reservoir — neither lake nor stream, but somewhere in between. The MEI expresses more precisely the trophic system of the lentic environment, that is, most of the primary productivity in the euphotic zone of the lake supporting higher trophic levels of organisms. Reservoirs vary with respect to lentic and lotic characteristics, hence the lower effectiveness of the MEI (developed for natural lakes) in estimating yield or biomass. The relatively small volumes and high flushing rates of some reservoirs place them in a lotic category, where production at the primary level is dependent for the most part on allochthonous detritus or sessile forms of algae and the contribution of indigenous primary production may be small at best (see Hynes 1970). Therefore, the efficiency of the MEI in these systems may be reduced proportionately to the increase of the ratio of the lotic to lentic characteristics of the reservoir. In all probability the decrease in MEI efficiency is created by the mean depth denominator (of the

---

[4] MEI (metric) = 3.281 MEI (English); the metric expression is therefore $Y \sim 0.966\sqrt{X}$ where yield is expressed as kg/ha per yr, $\bar{z}$ as metres and TDS as mg/liter (The remainder of the discussion will employ only the metric form of the MEI).

MEI), which becomes unimportant as an "expression of the nutrient sink effect" in reservoirs with small volumes and high flushing rates. This rationalization is supported by the large differences (*ceteris paribus*) in the correlation coefficients for standing crop on mean depth ($r = -0.163$; df = 108) in Jenkins' (1967) study, and yield on mean depth ($r = -0.830$; df = 22) from Ryder's (1965) data. The former was not significant at the 0.05 level whereas the latter was highly significant ($P<0.01$).

A second notable difference between the logarithmic plots of Jenkins' (1967) data and those of Ryder (1965) was the obvious curvilinear relationship of the former as opposed to the apparent rectilinearity of the latter (Fig. 1). Ryder's data, however, covered a relatively small range (MEI varied from 0.3 to 65). Jenkins' reservoirs, some of which had total dissolved solids as high as 2200 mg/liter, had a proportionately larger MEI range (0.7–1600). If the 0.3–65 range of Ryder's data were used as outside limits for Jenkins' regression, then the latter could also be approximated satisfactorily by a straight line. Indeed, an MEI of about 100 seems to express an optimum point of high total dissolved solids and correspondingly low mean depth beyond which might occur a salinity sufficiently high to inhibit the osmoregulatory or ionoregulatory processes of certain freshwater fish species and hence to exert osmotic or ionic stresses and resulting lower rates of production. Conversely, excess concentrations of ions that are essentially unrelated to fish yield (e.g. sulphates, chlorides) may result in an MEI overestimate of yield when such MEI exceeds 100.

In a later paper Jenkins (1970) suggested that the morphoedaphic expression was useful for estimating reservoir fish production. Maximum crops were represented by indices of from 16 to 100. The MEI accounted for 62% of the variability in crops of hydropower storage reservoirs. Jenkins and Morais (1971) found that lakes with low MEI values have proportionately higher standing crops of sport fishes than lakes with high values. At an MEI of 3, a lake's fishes comprised about 60% sport species as compared to 35% at 30, 25% at 300, and only 20% at an index value of about 3000. The MEI was thus indicative of a qualitative as well as quantitative aspect of the fish crop.

A further extension of the MEI ensued with its application to a series of seven central African Lakes (Regier et al. 1971). For the set of data available, Ryder's (1965) linear model and Jenkins' (1967) curvilinear model provided equally good fits. In both cases the data were first transformed logarithmically. But at a particular value of the MEI the curves for the African data lay approximately an order of magnitude (base 10) above the line for north-temperate lakes and a considerably lesser amount above the U.S. reservoir yield curve (Fig. 1).

A recent application of the MEI applied to a series of 46 north-temperate Finnish lakes (raw data from J. Toivonen personal communication) produced a highly significant linear regression closely parallel to that of Ryder (1965) and only slightly above the line for North America (Fig. 1). For these sets of data from the three climatic regions, the fitted relation, whether curve or straight line, were of similar slope but were offset with respect to the yield variable at fixed MEI. The curvilinear plots showed downward deflection at approximately the same point on the abscissa.

More recently an apparent relation between primary production and the MEI was described for a series of African lakes (Henderson et al. 1973), but its fit was not close. The authors inferred from the differences in slope between regressions of primary production on the MEI and fish yield on the MEI, that fish yield increased as a power function of primary production. They interpreted this observation to be a result of low trophic transfer efficiencies in waters of low primary productivity, and high efficiencies in water high in primary productivity.

In the same paper a hypothetical model depicting the relation between yield and the MEI for a world system of lakes was described. It was based on the previously described systems of Ryder (1965, 1972) for north-temperate lakes; Regier et al. (1971) for African lakes and reservoirs, and Jenkins (1967) for temperate reservoirs. The remaining curves were determined on the basis that the fish yield at fixed MEI was approximately proportional to differences in latitude between the six climatic zones. Differences in yield among the six lake sets were thought to depend primarily on variability in the lengths of growing seasons when the MEI was held constant.

Since its first description, the MEI has been utilized as a yield or biomass estimator for lakes belonging to several different global systems, e.g. yield to California sport fishery (Cordone and Frantz 1966); ichthyomass and yield in African reservoirs (Balon 1972; Ryder 1973); potential standing crop of monsters in Loch Ness (Sheldon and Kerr 1972); and yield at various geological successional stages of a lake by dominant taxa (Colby et al. 1972). Other attempts have been made (with moderate to poor success) to relate the MEI to waterfowl production, eutrophication level, density of water-dependent aboriginal populations, or as an indication of the limits to summer cottage development on inland lakes (Harvey and Fry 1973). Poor relation may in part have resulted from the failure of accurate quantification of the biotic component in the MEI equation.

Criteria for Use

Some of the criteria for use of the MEI as initially inferred by Ryder (1965) from his data set suggested that treated lakes be relatively large in surface area (>260 ha); be located in the north-temperate climatic region at altitudes less than 600 m; and have several years of catch records resulting from moderate to intensive fishing pressure. It was also recommended that lakes subjected to anomalous environmental or biological conditions be excluded from regression treatment. Some of these conditions are: excessive pollution, high flushing rate, extreme inorganic turbidity, excessive water-level fluctuations, extensive winter or summer kill, alternate year spawning, and extensive epizootic mortality.

Subsequent experience in the use of the MEI, especially that of Jenkins (1967) and Regier et al. (1971) has resulted in less rigorous criteria for application and more flexibility in its use. Present criteria for establishing a family or set of lakes suitable for regression treatment of yield on MEI require only that the lakes in the set be subjected to a relatively homogeneous set of environmental conditions, with the exception that those morphological and edaphic variables represented by mean depth and total dissolved solids may include a wide range.

More specifically, the requirements are: 1) relatively homogeneous climatic conditions within the set; 2) stoichiometry within the ionic spectrum resulting in fairly constant ionic ratios; 3) approximately proportional flushing rates per unit of lake volume (includes drawdown considerations); 4) inorganic turbidity on the same order of magnitude for all lakes in the set; 5) moderately intensive to intensive fishing effort on a spectrum of species for a number of years. Lakes subjected to regression analyses on the basis of these criteria but deviating substantially from the regression line may be suspected to be under the influence of an atypical environmental or biological condition. The use of the MEI then may provide additional service by emphasizing the existence of the anomaly, which may not be obvious from a cursory limnological examination.

FISHING EFFORT

The yield criterion which requires that lakes be subjected to moderately intensive to intensive fishing pressure has been of concern to investigators. Ricker (1954) shows that for a single stock, equilibrium yield is near the maximum over a wide range of exploitation rates. In a multi-species fishery, it would be expected that maximum equilibrium yield may be closely approximated over a wider range of effort because of various compensatory factors and species interactions that ensue with increased fishing effort. Low effort might not be expected to activate some of the density-dependent, compensatory factors (increased growth, decreased natural mortality, increased recruitment). Moderate to intensive effort however may induce a perturbation into the system that would move the equilibrium yield towards the maximum. Once the maximum equilibrium yield was achieved, increased effort would tend to push the total resiliency of the system to its outer limits without increasing yield, and further effort beyond this point would produce again a smaller yield (Regier and Henderson 1973; Regier 1973). In effect, any fishery that takes different species relatively opportunistically and is sufficiently intense to bring about marked changes in growth rates, natural mortality rates, recruitment or changes in relative abundance in a multi-species fishery might be considered as sufficiently intense to satisfy our criteria.

Socioeconomic clues may be useful also in determining fishing intensity. Lakes with commercially valuable species and located close to major markets are usually fished intensively. In such situations, commercial fishermen show a resiliency of their own to respond not only to fish abundance but also to market demand and price structures. Extra effort may be applied during seasons of scarcity for some species, religious holidays, or other situations likely to increase demand and consequently prices. Superimposed on the socioeconomic structure of a fishery is the ever increasing technological competence of the fishermen and their gear, which allows them to respond quickly and effectively to changes in prices and demand.

Consideration of the effort criterion thus need not be based strictly on biological factors but may also utilize socioeconomic evidence. The difference between yields produced by a moderately intensive fishery and a very intensive fishery on a long-term basis are likely to be slight. Even overexploitation resulting in smaller yields is usually compensated for by large yields at the beginning of a new fishery, and long-term averaging will result in yield estimates approaching the maximum equilibrium yield in a moderate- to intensive-effort fishery.

The Components of the MEI

TOTAL DISSOLVED SOLIDS

Often known as filtrable residue or residue on evaporation, TDS is determined by filtration and evaporation. The residue after evaporation is dried to a constant weight in an oven at 103–105 C and weighed (Am. Publ. Health Assoc. 1960). Lakes with high levels of inorganic turbidity in the form of colloidal clays often require further processing to remove all suspended solids. The final weighing is expressed as parts per unit of mass or volume of water (the distinction is negligible in fresh waters). It is recognized that some bicarbonates and organic matter may be decomposed by the heating process (Rawson 1951).

Kemp (1971) has stated that TDS is of greater importance than chemical composition in any classification of waters from a practical standpoint and it has often been assumed that total dissolved solids are proportionate to one or more of its vital, or limiting component parts such as carbon, phosphorus, or nitrogen (Rodhe 1949; Hutchinson 1957, p. 558; Vollenweider 1970, p. 71; Stumm and Morgan 1970, p. 430). Although some samples or local anomalies may produce seeming exceptions to this observation, as a general rule it is useful to know that a lake has high or low total dissolved solids (or any of its correlates such as conductivity or total alkalinity). Consequently, as an indicator of fish yield, total dissolved solids may be more useful than any of its single component ions, which may be more subject to variations in time and space or biological flux.

The fact that an instantaneous major change in a limiting ion (phosphorus for example) would not immediately change the level of total dissolved solids noticeably, because the magnitude of the latter, commonly 10^4 times that of phosphorus, is irrelevant in a natural system. The same abiotic effects that will contribute to significant changes in phosphorus concentrations will likely in time affect total dissolved solids significantly and proportionately. Some of these major exogenous influences may be due to meteorological or hydrological conditions that contribute to, or dilute all nutrients within the basin proportionately. It has been reported by Gibbs (1970) that the major mechanisms controlling water chemistry are precipitation, rock dominance, and the evaporation–crystallization process. Biological cycling of phosphorus or other limiting nutrients does not consume the ion, but returns it to the system (Rigler 1964). Consequently, a low value of phosphorus may not in itself indicate a low productivity, but perhaps a high productivity due to a rapid assimilation of all available phosphorus in the system. In such a system, inadequate sampling of phosphorus might mislead the investigator into the belief that he was dealing with an unproductive system, whereas total dissolved solids would be essentially unaffected by phosphorus fluctuations and would serve as a better general indicator of the productivity level of the lake.

A correlation of TDS and yield, in itself, does not shed light on the nature of the causal interconnections. David Lean (personal communication) suggests that at least some fraction of TDS exists as a consequence of fertility. This fraction may result from polymerization of specific organophosphates excreted by microorganisms. If this is so, the precision of the MEI may be improved by measuring only that fraction of TDS that is a result of ecological productive processes. The new model derived may then approach the precision of a deterministic model as opposed to the present empirical model represented by the MEI.

The importance of dissolved nutrients in lake waters has been emphasized by Naumann (1932) and has since been investigated by a legion of limnologists (e.g. Rawson 1951). TDS represents an average edaphic condition for any watershed, as chemically it proportions the effects of various soil and geological conditions as reflected by both allochthonous and autochthonous dissolved minerals. Its seasonal variability seems to parallel, at least to a certain degree, seasonal variations in productivity. Once the seasonal variability of this measurement is understood for any set of lakes, sampling can be reduced to that time of year representing the mean annual condition. For north-temperate lakes, a single surface water sample taken towards the end of July or in the first week of August closely approximated the mean TDS value for the whole year (Ryder 1964). This was dependent on negligible wind and rainfall for about one week prior to the time the sample was taken.

TDS may also be representative of certain climatic effects. Hence, lakes in regions with long, cold winters often have lower TDS than the edaphic condition would indicate, because of the relatively short period of time available for the dissolution and transportation of allochthonous minerals to the lake (autochthonous minerals, however, may be concentrated in the water column under similar circumstances). Some tropical lakes, on the other hand, may receive almost continuous supplies of nutrients through underground springs or runoff in regions of high precipitation. A single determination of TDS or an annual mean should be considered only as a static or instantaneous value reflecting the true dynamic condition in which nutrients are constantly flowing into, out from, and within the system. In this respect TDS probably bears the same relation to nutrient loading (Vollenweider 1969) as standing crop of fishes bears to actual fish production.

TDS may reflect other environmental features, such as physiography, shore development, quantitative and qualitative effects of the terrestrial vegetation on the surrounding watershed, or aerial fallout of nutrients. Although these effects may be difficult to evaluate individually, they are proportioned, however subtly, in a single TDS determination representative of the epilimnion in dimictic lakes or of the mixolimnion in meromictic lakes. This determination is usually obtained at a point remote from shore and in the surface waters, where considerable mixing takes place through internal or wind-induced currents.

Conductivity (Hutchinson 1957, table 69) and total alkalinity (Ryder 1964) are significant correlates of TDS that may be substituted for the latter in the MEI when TDS readings are not available. Both of these variables will give similar results when used in yield regressions. Suspended solids may be a useful correlate as well (see Sheldon et al. 1972, for explanation) and may be the preferred variable in marine systems.

MEAN DEPTH

Mean depth is defined as the volume of a lake divided by its area (Hutchinson 1957). It is sometimes determined by other methods (Neumann 1959) or by simple arithmetic averaging of depth transects prorated per unit of area. Rawson (1955) has stressed mean depth as a most important morphometric feature of a lake. Its inherent value as an estimator of yield, however, is somewhat obscured by the multiplicity of effects it engenders.

Mean depth represents other morphometric features of a lake than depth alone. To a degree it correlates inversely with the extent of the "euphotic-littoral" zone, that is, that depth stratum of a lake which not only allows adequate light penetration for the growth of planktonic algae, but is also sufficiently shallow in the shoreward regions to provide attachment surfaces for sessile algae and macrophytes within the euphotic zone. In addition, benthic animals may be more abundant in shallow waters where plants proliferate and dissolved oxygen is abundant. More attachment surfaces for aufwuchs are likely to occur in shallow waters and more shelter and food for benthic organisms.

Mean depth is also an inverse correlate of shore development. Lakes with a high shore development factor or high degree of insularity will generally be shallower than lakes with uniform shorelines and low numbers of islands. Mean depth is a more obvious direct correlate of area (Hayes 1957) and an exact correlate of volume when area is held constant (by definition). Consequently mean depth is representative of several morphometric features of a lake other than depth alone.

Mean depth may also give a clue to past processes that have contributed to the potential productivity of a lake. Most of the North American Pleistocene glacial lakes, scooped from soft nutrient-rich sedimentary rocks, are typified by shallow waters and relatively high productivity as compared to lakes of the Precambrian Shield which are in deep basins of nutrient-poor igneous rock, and consequently, less productive (Ryder 1964).

The distinctive inflection in the mean depth curves inferred by Rawson (1955) at about the 18-m level suggests a secondary effect beyond the limiting effects of the trophogenic zone of a lake which for his north-temperate dimictic series usually occurred in the upper 10 m. It seems likely that the water mass below this level (18 m) serves as a "nutrient sink" and removes nutrients from the trophogenic zone in the form of settling seston and phytoplankton, at least for most of the year when density stratification is in effect. The nutrient-sink concept explains more fully the fish yield differences between Lake Erie and Lake Ontario which have comparable nutrient values, than do volumetric differences or dilution factors alone. Lake Tanganyika in Africa, with its extremely high TDS in the lower water strata and relatively low levels in the surface waters is an extreme example of a nutrient sink where some nutrients are lost to the system for an indefinite period (Beauchamp 1939). Large areas of demersal waters of the Baltic may also act as a nutrient sink (Fonselius 1970).

Two other major effects of mean depth are its role in the modification of the climatic and edaphic regimes. Deep lakes are usually colder during the growing season than shallow lakes in the same climatic setting if we assume a homogeneity of other variables on which water temperature is dependent. Similarly, *ceteris paribus*, where the edaphic condition is uniform for a deep and a shallow lake, the deep lake will normally have lower nutrient levels (as indicated by TDS) when an annual mean is computed.

Mean depth may also be related to mixing depth (epilimnion), the upper stratum of a lake that consists of uniformly warm, circulating and fairly turbulent water (Hutchinson 1957). This zone of a lake is superimposed on the euphotic zone, and these together provide the most productive lake stratum. In reservoirs and marine systems, mixing depth may be a more useful indicator of biological processes than mean depth per se (Jenkins 1967; Hargrave 1973).

In summary, while the inherent significance of TDS and mean depth is imprecise or even vague, it is of paramount importance to recognize that neither one of these apparently simple measurements is representative of only one environmental variable, but rather depicts a whole complex of interrelationships in the ecosystem.

Related Models

Clearly, any of a number of different morphometric and edaphic factors could at times be paramount in determining the productivity of a given lake or set of lakes. We earlier inferred that the robustness of the MEI stems from a choice of parameters which successfully integrate the effects of a relatively large number of factors, any of which could be individually limiting in a given instance. If so, it follows that different morphometric and edaphic parameters could be used to formulate numerous variants of the MEI, each of which could be useful for describing the productivity of particular sets of lakes. That is, the MEI itself is but one formulation, albeit a deliberately generalized one, of a larger family of related models. By this reasoning, alternative productivity indices that incorporate morphometric and edaphic parameters can be shown to be congruent with the MEI.

Such is the case with several published indices which permit lakes to be ranked according to yield potential or degree of eutrophy (Vollenweider 1968; Schindler 1971; Hargrave 1973). It is instructive to examine the relations of these models to the MEI.

Vollenweider (1968) proposed a method for determining admissable and dangerous levels of nutrient loading. His concept was realized in the form of two equations which specify the two loading levels for nitrogen and phosphorus respectively (Schindler et al. 1971). The equations are of the form

$$L = a\bar{z}^{0.6} \qquad (1)$$

where L represents the specified nutrient loading level (mg/m^2 per yr) and a is a coefficient appropriate to the designated nutrient and loading level.

By this reasoning, the degree of eutrophy expected in a lake varies directly as the level of nutrient loading, but the effect of loading level is in turn ameliorated as a power function of the mean depth of the lake. That is, eutrophy varies directly with loading level and inversely with mean depth;

$$P = \frac{cL}{\bar{z}^{0.6}} \qquad (2)$$

where P indicates degree of eutrophy and c is an appropriate coefficient.

If, due to ecological processes, TDS is roughly proportional to loading level L in equation (2) (see the preceding discussion on this subject), then the congruence of Vollenweider's model with the morphoedaphic index is clear. The power index of 0.6 assigned to $\bar{z}$ in Vollenweider's model is similar to the comparable value (0.45) determined by Ryder (1965) for $\bar{z}$; the only marked difference between the two models may be in the numerators. If L, on average, is proportional to TDS$^{0.6}$ (or TDS$^{0.45}$), then the two models are close equivalents.

The index described by Schindler (1971) fits a similar pattern. Schindler (1971) supposed that the rate of supply per unit volume of lake water of a limiting nutrient affects various properties related to lake productivity or eutrophy. He assumed that precipitation was homogeneous over the set of experimental headwater lakes he analyzed, and that it was the major source of limiting nutrient. Specifically, he inferred that the rate of supply of the limiting nutrient is proportional to the terrestrial area of a lake's watershed (A_d) together with the surface area of the lake itself (A_o). Concentration of the limiting nutrient supply in the lake is then expressed as

$$\frac{A_d + A_o}{V} \qquad (3)$$

That is, Schindler proposed that the rate of supply of limiting nutrient to a lake ecosystem is directly proportional to the catchment area, and inversely proportional to the volume of the lake. In support of this view, various parameters that would be expected to vary with nutrient supply were shown to vary in proportion to expression (3) for the experimental lakes he analyzed (Schindler 1971a).

In Schindler's model, $A_d + A_o$ is used to represent the rate of supply of the critical nutrient. Ryder's model used TDS to represent the nutrient factor. The two models are related if

$$\mathrm{TDS} = K(A_d + A_o)$$

where K is a dimensionally correct coefficient, because by recalling that $V = \bar{z}A_o$, we can then write

$$\mathrm{MEI} = \frac{\mathrm{TDS}}{\bar{z}} = \frac{K(A_d + A_o)A_o}{V} \qquad (4)$$

The right hand side of the equation (4) is a modified form of Schindler's model, but because $\bar{z}$ and A_o are correlated variables, the two models are similar but differently scaled.

Hargrave (1973) has observed that benthic respiration is related to primary production (both expressed as carbon equivalents in g Cm^{-2}yr^{-1}) and depth of the mixing zone in the familiar form of a power function. That is,

$$C_o = a\left(\frac{C_i}{z_m}\right)^b \qquad (5)$$

where C_o is sediment respiration, C_i is primary production, z_m is mixed-layer depth, and a and b are fitted coefficients. The slope coefficient $b = 0.64$ estimated by Hargrave approximates the values determined for the MEI. If we assume that primary production expresses the nutrient factor in parallel with TDS, and that z_m and $\bar{z}$ are associated expressions of the morphometric factor, then equation (5) is a variant of the MEI, in the sense that benthic respiration and fish yield exhibit comparable responses to morphometric and edaphic factors.

Taken together, the convergence of these and similar models on the familiar form of the MEI suggests that the index provides a general and relatively robust description of the principal factors regulating aquatic productivity. The fact that useful variations of the general form of the model have been derived doubtless reflects the expectation that different combinations of variables will yield the minimum residual variance for any specific set of observational data. That is, although the different variables used in the several variants of the model are correlated in some measure with their counterparts in the MEI, the scale factors and particular circumstances that characterize any given set of observations may be better expressed by one correlate than another for that particular set of measurements. By this reasoning, the morphoedaphic index can be regarded as a relatively generalized member of a family of congruent models.

Global Range of MEI

Knowledge of the global range of variables used to ascertain fish yield would contribute to the efficiency with which yield may be estimated for a single lake by compensating for differences in the length of growing season due primarily to latitudinal or altitudinal diversity. Consequently, 58 lakes for which data are available have been plotted on Fig. 2 on the basis of their relative MEI values (oblique lines), irrespective of their latitudinal and altitudinal locations. Lakes included in the graph were selected in part, to cover the known extremes of total dissolved solids and mean depth for North America, Africa, and Eurasia. Lakes with extremes in MEI were also selected, that is those with high TDS and low mean depth (Nebraska Lake) or high mean depth and low TDS (Waldo Lake). Additionally, many large well-known lakes were included as points of reference (e.g. African Great Lakes; Laurentian Great Lakes).

ENVIRONMENTAL AND PHYSIOLOGICAL LIMITATIONS

Superimposed on Fig. 2 are horizontal and vertical lines representing levels of environmental or physiological limitations to fish yield. These are not intended to be fully definitive, but represent some of the principal limitations to optimum elaboration of protoplasm in fishes, especially growth or reproduction but excluding variations in the length of growing seasons. Vertical line AA_1 ($\bar{z} =$ 5 m) segregates those smaller lakes that in north-temperate regions may winterkill during most years according to Nickum (1970), and therefore may not reach their full biotic potential every year. Other estimates of mean depth limitations on winterkill lakes with relatively long-term ice cover range from about 3 m (Schoenecker 1970) to 8 m (Sunde et al. 1970). Winterkill is related not only to the duration and opacity of ice and snow cover, but also to the total amount of organic matter within the system, and a precise depth limitation cannot be determined that will explain the variability among different systems. Lakes that are free perennially of ice-cover may similarly though less frequently be subjected to summerkill, (Ryder 1970), which may be equally devastating in reducing yield.

The second vertical line (BB_1) of Fig. 2 is Rawson's (1960) estimate of the mean depth of the trophogenic zone for a series of north-temperate lakes. It might be expected that north-temperate lakes no deeper than this 10 m limit would provide adequate attachment space within the euphotic zone for rooted aquatic plants or sessile algae, and allow photosynthesis to occur in a relatively large portion of the total lake volume. One might postulate then, that the most productive north-temperate lakes would fall between lines AA_1 and BB_1, whereas the most productive lakes in the warmer parts of the world might have a lesser mean depth than the 5-m level delimited by line AA_1. The optimum depth of African lakes subjected to lateritic turbidity would be considerably less than the comparatively clear north-temperate waters. This optimum depth may correspond with the depth of the euphotic zone as it is limited by inorganic turbidity. It may be difficult to separate the negative effects of inorganic turbidity from the homeostatic or self-limiting effects of organic turbidity, but it appears to be a fact that the most productive tropical lakes are the ones approaching zero in the vertical dimension (e.g. lakes Kyoga and George on Fig. 2), but still with sufficient depth to provide a satisfactory environment for growth and reproduction of fish species adapted to survival in that particular environment. Indeed, many ephemeral bodies of water in the tropics have a zero mean

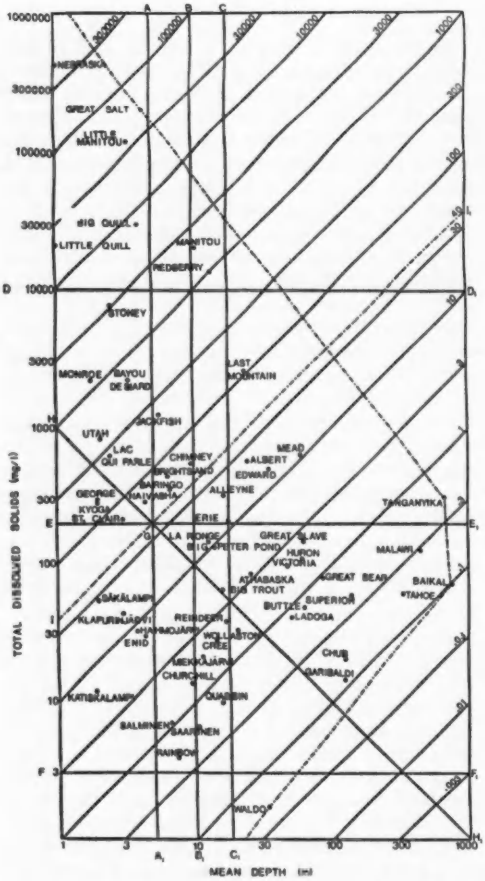


FIG. 2. Range of total dissolved solids, mean depth, and the morphoedaphic index (Ryder 1965) as indicated from 58 selected lakes from North America, Africa, and Eurasia.* The three horizontal and three vertical lines represent biotic or abiotic stresses as follows: AA_1 – Depth restriction of yield of north-temperate lakes through winterkill (Nickum 1970). BB_1 – Mean depth of trophogenic zone, north-temperate lakes (Rawson 1960). Primary production may be reduced drastically in strata deeper than this limit. This level may be different for tropical lakes. CC_1 – Limit of morphometric oligotrophy (Rawson 1952). Lakes deeper than 18 m have greatly reduced yields (see text). DD_1 – Upper iono- and osmoregulatory limits of most stenohaline freshwater species (Rawson and Moore 1944; Beadle 1969). EE_1 – Stoichiometric relations of major ions may cease (Hutchinson 1957, p. 554). FF_1 – Arbitrarily plotted. Low values of ions (e.g. Ca) may create ionic imbalance, increased energy expenditure and inefficient metabolism (Phillips 1959). Reproduction may be affected by lack of Ca for egg development (Hayes 1949) or inhibition of duration of sperm viability (J. M. MacMartin personal communication). Other notation is as follows: MEI – The morphoedaphic index is represented by the family of oblique parallel lines numbered from .003 to 300,000. HH_1 – The direction of maximum gradient of MEI values. II_1 – The optimum MEI ratio; $\frac{\text{TDS}}{\bar{z}} = 40$. Yields decrease as either end of this line is approached. G – The point of maximum potential yield on line II_1 – climatic effects not considered. Polygon (broken lines) – encloses expected global limits for mean depth, total dissolved solids, and consequently, the morphoedaphic index.

Location of lakes in Fig. 2.

Lake	*Location*
Albert	Uganda, Zaire
Alleyne	British Columbia, Canada
Athabaska	Alberta, Saskatchewan, Canada
Baikal	USSR
Baringo	Kenya
Bayou De Siard	Louisiana, USA
Big Peter Pond	Saskatchewan, Canada
Big Quill	Saskatchewan, Canada
Big Trout	Ontario, Canada
Brightsand	Saskatchewan, Canada
Buttle	British Columbia, Canada
Chimney	British Columbia, Canada
Chub	Province of Quebec, Canada
Churchill	Saskatchewan, Canada
Cree	Saskatchewan, Canada
Edward	Uganda, Zaire
Enid	Mississippi, USA
Erie	New York, Michigan, Ohio, Pennsylvania, USA; Ontario, Canada
Garibaldi	British Columbia, Canada
George	Uganda
Great Bear	Northwest Territories, Canada
Great Salt	Utah, USA
Great Slave	Northwest Territories, Canada
Hahmojärvi	Finland
Huron	Michigan, USA; Ontario, Canada
Jackfish	Saskatchewan, Canada
Katiskalampi	Finland
Klapurinjärvi	Finland
Kyoga	Uganda
La Ronge	Saskatchewan, Canada
Lac Qui Parle	Minnesota, USA

---

*Data from the following sources: Alexandrov (1959); Cordone and Franz (1966); Hutchinson (1957); Jenkins (1967); Kozhov (1963); the late R. H. Kramer (personal communication); Larson and Donaldson (1970); Martin (1955); McCarraher (1961); Northcote and Larkin (1956); Rawson (1960); Rawson and Moore (1944); Regier et al. (1971); Ryder (1965, 1972); J. Toivonen (personal communication); Welcomme (1972).

Ladoga	USSR
Last Mountain	Saskatchewan, Canada
Little Manitou	Saskatchewan, Canada
Little Quill	Saskatchewan, Canada
Malawi	Malawi, Mozambique, Tanzania
Manitou	Saskatchewan, Canada
Mead	Arizona, USA
Miekkajärvi	Finland
Monroe	Louisiana, USA
Naivasha	Kenya
Nebraska	Nebraska, USA
Quabbin	Massachusetts, USA
Rainbow	British Columbia, Canada
Redberry	Saskatchewan, Canada
Reindeer	Saskatchewan, Canada
Saarinen	Finland
St. Clair	Michigan, USA; Ontario, Canada
Säkälampi	Finland
Salminen	Finland
Stoney	Saskatchewan, Canada
Superior	Michigan, Minnesota, Wisconsin, USA; Ontario, Canada
Tahoe	Nevada, California, USA
Tanganyika	Tanzania, Zambia, Burundi, Zaire
Utah	Utah, USA
Victoria	Kenya, Tanzania, Uganda
Waldo	Oregon, USA
Wollaston	Saskatchewan, Canada

depth for a substantial portion of each year, yet may be highly productive of annual fishes such as *Nothobranchius taeniopygus* (Greenwood 1958) or aestivating species such as *Protopterus aethiopicus* (Poll 1953).

Optimum depth for maximum fish yields cannot be defined on a global basis except in general terms. In this respect optimum depth may be considered to be the least depth consistent with the physiological requirements of the major components of the indigenous ichthyofauna. Extremely shallow arctic waters, for example, may be highly productive at the primary production level, but because of anoxic conditions in the wintertime may be incapable of supporting a fish population. In another example, and at a higher trophic level, the lake trout (*Salvelinus namaycush*), a cold stenothermic species, may thrive in relatively shallow waters in the northern part of its range, (McPhail and Lindsey 1970), whereas extremely deep waters are required in its southern limits to maintain the temperature regime suitable for its growth and reproduction. It would be difficult then to define the optimum depth of a lake for maximum lake trout yield, without reference to climatic effects and the resulting physiological limitations.

In general, lack of success of relating primary productivity to ultimate fish yield (see Henderson et al. 1973) may stem from processes related to the physiological and ecological limitations of the fishes themselves. Hence the relation between primary productivity and nutrient loading may be assumed to consist of a shorter causal chain with fewer variables involved, resulting in a close correlation over a wide range of abiotic variability. The fish yield function, on the other hand, is exponential for several reasons. Fishes may be more rigorously limited by their physiological requirements than phytoplankton; their food web is often based on detritus of allochthonous origin, or terrestrial animals; abiotic factors affecting year-class strength may limit ultimate yield rather than nutrient or energy restrictions per se; and generally, a complex set of conditions are affecting the ultimate fish yield through a lengthy network of interrelations. The failure of even one of these vital relations could result in the loss of a species. However, in the application of the MEI, *total* fish yield is considered, and the drastic decline of one species may result in a compensatory explosion of another species, which will have a dampening effect on total yield fluctuations. This effect has apparently been observed in some of the Laurentian Great Lakes where whole species complexes have changed, but ultimate yield has remained approximately constant (Ryder 1965; Regier 1973). Ultimately, fish production is proportional to an index of primary productivity (MEI) irrespective of the trophic level at which production occurred (Kerr and Martin 1970).

Line CC_1 (Fig. 2) is the border at which morphological features of a north-temperate lake may overpower a favorable edaphic situation (Rawson 1952), and mean depth becomes an increasingly important factor in the estimation of fish yield. North-temperate lakes deeper than 18 m (mean depth) produce low fish yields even when total dissolved solids are optimum. Their larger hypolimnions serve as nutrient sinks, and store organic matter that is only partially exposed to the lake metabolism, twice a year in dimictic lakes, during the periods of overturn.

Line DD_1 delineates the upper osmoregulatory limits of most freshwater organisms (Beadle 1969) and is especially applicable to stenohaline freshwater fishes (Rawson and Moore 1944). However, osmotic stress is imparted to many freshwater fish species before the 10,000 mg/liter level of total dissolved solids is reached, resulting in lower yields due to a loss of efficiency in metabolic processes. By inspection of the curvilinear regressions of Jenkins (1967) and Regier et al. (1971), this occurs at an MEI of about 100, the point at which their standing crop and yield curves are deflected downward. Lakes with an MEI of 100 or greater generally have a TDS of 200 mg/liter or greater (Line EE_1) which is the level at which the stoichiometric relations of major ions may cease (Hutchinson 1957).

The effects of ion regulation are quite distinct from those of osmoregulation (Pora 1969), but on the basis of our present knowledge cannot be separated in the generalized graphic presentation in Fig. 2. F. E. J. Fry (personal communication) has suggested tentatively the term "ionosmoregulation" to describe the combined reactions until the individual effects have been defined adequately through experimentation.

The extremely low level of TDS (3 mg/liter) represented by line FF_1 has been arbitrarily plotted. The concentration of total dissolved solids is rarely so low in natural lakes, and lakes with higher levels of TDS usually are capable of supporting reproducing fish populations under a favorable set of other environmental conditions. Lakes with extremely low ionic concentrations may lack sufficient calcium for normal ion regulation, which may result in increased energy expenditure, a proportionately higher rate of metabolism (Phillips 1959), and lower production rates. Low levels of TDS may also set the lower limits for satisfactory reproduction of a species because ionic deficiency may prevent the water-hardening of egg capsules (Hayes 1949) or shorten the duration of sperm activity (J. M. MacMartin personal communication).

It follows from the above that lines AA_1 and EE_1 of Fig. 2 describe approximately the optimum conditions of depth and nutrients. If so, then the intersection of these two lines (G) would represent the optimum MEI (40) for protoplasm elaboration or ultimately, maximum fish yield. An optimum MEI range of about 40–100 may also be derived empirically from the standing crop curve of Jenkins (1967) or the yield curve of Regier et al. (1971). Lakes found in this general region of the graph may in their pristine condition have had a more diverse fauna because of the absence of abiotic stresses. These lakes may be considered to be primarily biologically accommodated (Sanders 1969) as opposed to saline lakes, for example, where abiotic stress is of foremost concern. Moving away from this optimum center (G) for biological homeostasis and maximum yield, we encounter greater abiotic stress in the form of dissolved salts at too high or too low a level for efficient ionic or osmotic regulation or reproduction, or extraoptimal depths which may have a dampening effect on the productive processes through the various channels described previously.

An optimum MEI of about 40, then, may be expected to be associated with high potential yield only when each of its component parts also approaches its optimum. A hypothetical lake with TDS of 20,000 mg/liter and a mean depth of 500 m would have an MEI of 40, but would certainly not support a reproducing population of freshwater fishes because of high osmoregulatory stress. Even on the assumption that fishes could tolerate and reproduce satisfactorily despite the high concentrations of salts, the extreme depth must limit the final yield to a low level. It is interesting to note, however, that there are no lakes on the graph representing both extremely high salt content and great depths. These do not appear to be common and are invariably devoid of freshwater fishes. The Dead Sea, a chloride lake with a maximum depth of 396 m (Gresswell and Huxley 1965) and a salinity of 226,000 mg/liter (Hutchinson 1957) is an example that comes readily to mind.

Again, if the intersection of AA_1 and EE_1 (G) on Fig. 2 provides optimum levels of dissolved nutrients and depth for maximum yield, and II_1 represents the optimum MEI line, then any point distant from G may be expected to produce lower fish yields per unit area (exclusive of the climatic factor), depending on the linear distance from G and, even more importantly perhaps, on the direction of the deviation from G. Potential yield from lakes close to oblique line HH_1 will drop as a function of their distance from G holding temperature fixed. This relation, of course, is simply yield as a function of the MEI (Fig. 1) which has previously been demonstrated for different sets of lakes (Ryder 1965; Jenkins 1967; Regier et al. 1971).

YIELD VARIABILITY WHEN MEI IS CONSTANT

With a deviation from G (Fig. 2) in any other direction than that of line HH_1, the potential yield is reduced, but to a lesser degree than when the line of travel is perpendicular to the family of MEI lines. This reduction of yield is least following along the parallel family of MEI lines, so much so in fact that it was impractical to show on the scale used in Fig. 2. However, Fig. 3A portrays a hypothetical curve for north-temperate lakes where MEI is a constant 3. If MEI is held constant, then TDS will vary proportionately to mean depth over a wide range of either component. From Fig. 3A, then, we would expect close to zero yield between the origin and FF_1, at which location minimum ionic requirements for fish reproduction and possibly ionic regulation would be satisfied. (This will vary greatly with species). Following the curve through AA_1 (optimum depth), we may expect a gradual yield increase proceeding towards EE_1 (optimum nutrient level). However, on this particular yield curve, CC_1 (morphometric oligotrophy) is transected before EE_1 and the combined effect is a reduction on potential yield. This dampening effect continues until DD_1 is reached, the upper limits of osmoregulation in freshwater fishes, at which point the total fish yield would rapidly approach zero.

It should be noted, however, that the line representing a MEI of 3 (Fig. 2) does not encompass lakes over the whole range shown on Fig. 3A. Consequently, assuming that the range subtended by Fig. 2 is representative of most of the world's lakes, then for MEI = 3 we could expect an actual range as approximated by the vertical lines JJ_1 and KK_1 (Fig. 3A). Actual yield variability due to deviations of the two component parts of the MEI from their optima would be much reduced and perhaps would be insignificant within the context of the MEI. Other effects on yield, such as exploitation rates or abiotic variables not presently under consideration (e.g. inorganic turbidity), could have a far greater influence on yield than the proportional variability of TDS and mean depth for any given MEI.

If we examine a second yield model at a higher MEI level (40), typical of many south-temperate and tropical lakes, a slightly different pattern evolves. As an MEI of 40 is optimal, that is, it is transected by both the optimal levels of TDS and mean depth, then optimal yield may be expected at this point (Fig. 3B). The mean depth of the trophogenic zone will probably have a different value to that for north-temperate lakes, but any effect on ultimate yield could be expected to be similar. Yield (Fig. 3B) could be expected to decline after crossing lines AA_1 and EE_1, which represent optimal levels of TDS and mean depth. The rate of decline would increase after the level of morphometric oligotrophy (CC_1) is passed until the upper limits of osmoregulation are reached, at which point potential yield reaches zero. Again, the actual range encompassed by the world's lakes (between JJ_1 and KK_1) represents a relatively small range of yield values.

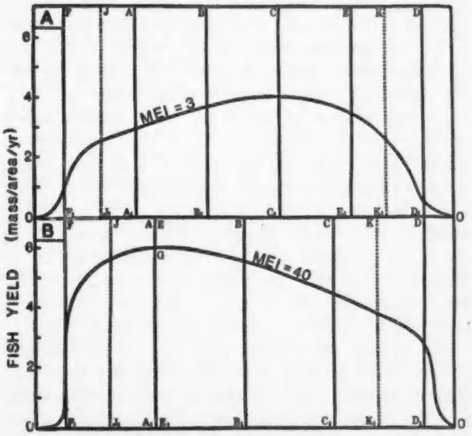


FIG. 3. Selected morphoedaphic index curves (MEI = 3, Fig. 3A and MEI = 40, Fig. 3B) where the ratio of TDS to mean depth remains constant throughout the range although the absolute values of these components vary. The y axis has been greatly magnified to show small differences on the ordinate scale relative to large magnitudes on the abscissa. The solid vertical lines show the effect of abiotic stresses on yield potential. The broken vertical lines represent the actual global range of lakes for the two MEI values as depicted in Fig. 2. Within this range only very small yield differences are expected.

A similar pattern of yield values may be postulated for any given MEI, the yield reaching the maximum level close to the optimum values of TDS and mean depth, and minimal values as FF_1 and DD_1 are approached, representing hypothetical lower limits of ion regulation and upper limits of osmoregulation in freshwater fishes. Actual yield variation for any single MEI may be empirically determined once sufficient data are available.

LAKE CHARACTERISTICS

Many of the lakes included in Fig. 2 were selected to depict as wide a range of TDS and mean depth as possible, and combinations thereof resulting in a correspondingly wide range of MEIs. Included on the graph are lakes less than 1 m mean depth to the world's deepest lake, Lake Baikal, with a mean depth of 730 m (Hutchinson 1957, p. 168). Total dissolved solids range from 1.7 mg/liter in Waldo Lake, Oregon, possibly one of the most oligotrophic lakes in the world (Larson and Donaldson 1970), to an unnamed sulphate-bicarbonate lake in Nebraska with total dissolved solids reaching 448,000 mg/liter (McCarraher 1961). Not surprisingly, these two lakes have the lowest and highest MEIs respectively, Waldo with 0.04 and the Nebraska lake with about 448,000. The Nebraska lake cannot support a fish population because of its high salinity and ionic imbalance. Waldo Lake, on the other hand, contains two species of salmonines and a cottid (D. W. Larson, personal communication) although apparently at extremely low standing crop levels. Introduction of trout fry into Waldo Lake usually results in high mortality within a few days. The reason for this is not clear, but it has been postulated that one of the major ions may be limiting in Waldo Lake with corresponding restrictions in food supply. Subsequent tests in which phosphorus, nitrogen, and carbon were added to Waldo Lake, both alone and in combination, suggested that phosphorus was the only limiting ion with respect to algal growth (Maloney et al. 1972; Powers et al. 1972). As these investigators were not concerned with factors limiting fish yield, however, they did not note the extremely low levels of calcium recorded from Waldo Lake by Larson and Donaldson (1970). A calcium concentration of only 0.086 mg/liter could be considered to be limiting in two ways. It could create stress by inhibiting efficiency of ion regulation in fishes, or it could prevent reproductive success because of insufficient calcium for the water-hardening of egg capsules (Hayes 1949) or high levels of sperm activity (J. M. MacMartin personal communication). The ultimate effect may be the survival of only small numbers of progeny, with a correspondingly low demand on available nutrients. This in turn could insure the perpetuation of a fish population, albeit at extremely low standing crop levels, rather than the likelihood of the available food supply being utilized in a short period of time by a single large year class which may result in the extinction of the whole population. Low calcium levels, then, may be considered as an abiotic compensatory factor that retains fish population levels at optima and guarantees ecologic homeostasis even at extremely low biomass levels.

Lake Baikal (MEI = 0.1) has a low yield despite a relatively intensive fishery (Kozhov 1963). Several deep, oligotrophic lakes of the north-temperate region are grouped closely together (Fig. 2) and have fish yields of low magnitude. Lakes Tahoe, Superior, Great Bear, Great Slave, Huron, and Ladoga are all large lakes producing yields of about 0.5–2 kg/ha. Lake Victoria, East Africa, is a tropical representative of this group of lakes, whose favorable climate results in an annual yield of 14 kg/ha (Regier et al. 1971) — a low yield for a tropical lake. At least two other of the African Great Lakes fall into this category. Lakes Tanganyika and Malawi (Nyasa) are among the world's deepest (Hutchinson 1957, p. 168) and their MEIs are correspondingly low. Again we might expect a higher potential yield from these lakes than that for a north-temperate lake with similar morphometric and edaphic features.

Clustered about line CC_1 (Fig. 2) is a group of moderately large to large north-temperate lakes, generally shallower than the previous group and with higher yields for the most part. Lakes La Ronge, Big Peter Pond, Athabaska, Big Trout, Reindeer, Wollaston, and Cree have fish yields ranging from 0.75 to 7.5 kg/ha annually. Variation within this group may result primarily from the broad range in MEI (about 1–10) covered by this group of lakes (Ryder 1965) as well as variables of climate and exploitation rates.

Towards the centre of Fig. 2, we find two extremely high-yield, north-temperate lakes, Erie and St. Clair. These lakes produce fish yields on the order of 10 kg/ha annually, when both their sport and commercial yields are totalled. Lake Kyoga and Lake George are two highly productive African lakes, with annual yields well over 100 kg/ha (Regier et al. 1971). African Lakes Baringo and Naivasha have lower MEIs and proportionately lower yields. Although this may seem to contradict the establishment of MEI = 40 as optimum, in reality the optimum as empirically determined from the curves of Jenkins (1967) and Regier et al. (1971) would tend to cover a range of from 40 to about 100, and considerable latitude is available for the accommodation of physiological and ecological processes before productivity is affected and yield reduced.

The lakes above DD_1 (Fig. 2) are all carbonate, sulphate or chloride saline lakes. Successful introduction of lake whitefish (*Coregonus clupeaformis*) and walleyes (*Stizostedion vitreum*) have been made in Redberry Lake (Rawson and Moore 1944). The Quill Lakes, both formerly with native fish populations, are now depauperate because of increasing salinity. Only the ninespine stickleback (*Pungitius pungitius*), a euryhaline species, has survived in Little Quill Lake (Rawson and Moore 1944). The remaining lakes above DD_1 are bereft of fish populations, but may support invertebrate species. Several saline lakes below DD_1 support viable fish populations (Stoney, Last Mountain, Jackfish, Brightsand) and the latter two are exploited commercially (Rawson and Moore 1944).

The temperate reservoirs of Jenkins (1967) are scattered over a wide range of MEIs (Fig. 2) and are representative of equally wide ranges of yield. Only one of these, Lake Mead, with a mean depth of 60 m can be considered as deep. The remainder — Bayou De Siard, Monroe, Utah, Lac Qui Parle, Enid, and Quabbin — are all less than 16 m mean depth, but have a rather wide range of TDS (10–220 mg/liter). The eight shallow Finnish lakes, all in the lower left-hand quadrant (Fig. 2) are representative of Fennoscandian oligotrophic and dystrophic lakes (Järnefelt 1952) of low to moderate yield potential (J. Toivonen personal communication).

No doubt, lakes exist outside the MEI range encompassed by Fig. 2. Almost certainly there are shallow dishes scoured out of Precambrian rock by Pleistocene glaciation with demineralized water in various parts of the world, particularly the northern hemisphere. These lakes would fit on the extreme lower left quadrant of Fig. 2, but would likely be depauperate of fishes because of climatically induced physical limitations. Deep lakes ($\bar{z} > 60$ m) with a high TDS content (>10,000 mg/liter) also are lacking from Fig. 2. This type of lake, possibly represented by the Dead Sea, is not a common component of the global family of lakes. The total range of lakes, of most general concern to those interested in regional limnology is enclosed by the polygon connecting Waldo, Baikal, Tanganyika, and Great Salt lakes (Fig. 2), which also subtends an MEI range of about 0.04–448,000.

Special Applications of MEI

Prediction of Angling Yield

In utilizing the MEI for the prediction of yield to anglers, it is useful to segregate a set of lakes geographically associated with somewhat similar (though not necessarily homogeneous) fish populations, and subjected to exploitive pressure from the same angling faction. This faction might well be heterogeneous in its methods but generally exert the same type of stress, both quantitatively and qualitatively on all lakes in the set. It is not essential that all lakes in the set be subjected to the same rates of exploitation, but only that sufficient exploitation of game species takes place to set in motion the compensating density-dependent effects.

A set of lakes that might be expected to meet these criteria has been described by Martin (1966) and Fraser (1972). These are small- to medium-sized lakes (8.9–6000 ha) located on the Precambrian Shield in Algonquin Park, Canada. Their major gamefish components consist of one or more salmonine species including *Salvelinus fontinalis*, *S. namaycush*, *S. fontinalis* × *S. namaycush*, and *Salmo gairdneri*. Species diversity is low in all these lakes and generally low nutrient input has resulted in low to moderate yields ranging from 0.28 to 8.4 kg/ha.

Plots of yield to the angling fishery on the MEI resulted in a linear relation following logarithmic (base 10) transformation (Fig. 4). Billy Lake, which deviated substantially from the line, was the only lake that did not exhibit sharp thermal stratification by midsummer (Fraser 1972) and was known to contain large standing crops of unexploited yellow perch (*Perca flavescens*) and white suckers (*Catostomus commersoni*) in addition to small numbers of pumpkinseeds (*Lepomis gibbosus*) and brown bullheads (*Ictalurus nebulosus*). The only native game fish species inhabiting the lake (*Salvelinus fontinalis*) had limited natural reproduction, and planted salmonines resulted in poor returns to the creel (Fraser 1972). It may be fair perhaps, to suggest that Billy Lake did not meet our criteria for a homogeneous group of lakes, but it is more useful to speculate on and eventually to determine the causes for its deviation in expected yield from the remainder of the set.

The lake deviating furthest from the line, Little Minnow, also had the highest yield, and lacked white suckers, pumpkinseeds, brown bullheads, and yellow perch (at least until 1967 for the latter species). This lack of competitive interacting species was noted by Fraser (1972) as a suitable explanation for the abnormally high yield for Little Minnow Lake.

Generally, regression treatment of a homogeneous group of lakes such as this will provide clues as to the successfulness of management practices towards optimizing a sport fishery.

An Indicator of Ecological Stress

It was previously specified, for sulphide and chloride lakes, that the MEI may prove to be an indicator of biological stress when regressions of yield or biomass on the index assume a negative slope. Data provided by Viitanen (1971) from six

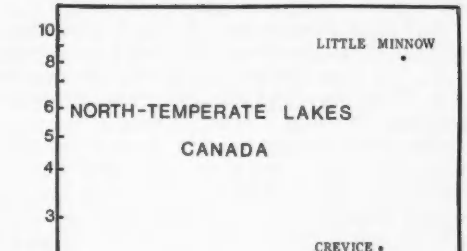


FIG. 4. Angling yield related to the morphoedaphic index for a relatively homogeneous group of nine Precambrian lakes in Algonquin Park, Canada. The component parts of the MEI cover only a small range for this group of lakes (TDS — 28–54 mg/liler; mean depth — 4.6–8.8 m; MEI — 2–10). Data were taken from Martin (1966) and Fraser (1972).

stations on a transect progressing from a shallow inner bay (Laajalahti) near Helsinki, and proceeding towards the deeper, outer waters of the Baltic proved useful in demonstrating environmental stress on bottom fauna. Biomass estimates of bottom fauna at each of the six stations were made once a month from May to October and a mean taken for each station for this period (Viitanen 1971). In this instance the MEI comprised mean suspended solids at each station (assumed to be a correlate of TDS), divided by the depth of the station. (The use of suspended solids in the numerator of the MEI in place of TDS was justified by extending the observations of Sheldon et al. (1972) to include dissolved materials. Hence it is assumed that a proportionality exists between TDS and suspended solids).

An inverse relation resulted (Fig. 5) when mean biomass of bottom fauna was plotted against the MEI. The three shallow (2–3 m) stations near A (Fig. 5) all supported standing crops of bottom organisms less than 1 g/m^2, whereas at the three deeper (8–29 m) stations (B) biomass exceeded 100 g/m^2. Closer investigation revealed that daytime oxygen saturation at the three shallow stations ranged from 26–149%, and had early morning readings been taken no doubt the lower level would have diminished further. Oxygen supersaturation was known to occur at all three shallow stations (Viitanen personal communication) with its known adverse effects on certain organisms (Macan 1963). Blue-green algae (Myxophyceae) also proliferated at these three stations and the toxins produced (Davis 1955) may also have had an adverse effect on some of the invertebrates.

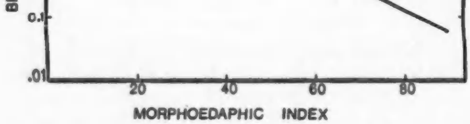


FIG. 5. Invertebrate biomass (from substrate) for six stations on the Baltic proceeding from a small inner bay near Helsinki (A) to the outer Baltic waters (B). The inverse relationship of standing crop to the MEI results from abiotic stress conditions in the inner waters. Data from Viitanen (1971).

The three deeper stations more remote from shoreward effluents produced oxygen saturations ranging from 66 to 98%, not as extreme as the shallow stations and more ameliorative to most benthic organisms. Blue-green algae were not abundant at these stations. The differences in standing crops of bottom invertebrates between the deep and shallow stations amounted to more than three orders of magnitude (Fig. 5), and may be ascribed to differences in dissolved oxygen concentrations and its biotic effects or due to toxins produced by blue-green algae in the shallows. The negative slope of the biomass line (Fig. 5) may be equated to the descending limb of Jenkins' (1967) ichthyomass curve, in which production was reduced by high salinity which in turn inhibited osmoregulatory processes of freshwater species.

Changing Environments

ZUIDERZEE-IJSSELMEER

The Ijsselmeer, a large freshwater lake in the Netherlands, was formed from the Zuiderzee by diking the confluence of the latter with the North Sea and allowing fresh water from the Ijssel River to flush out the brackish water. Chlorinity levels changed from 6‰ (6000 mg/liter) prior to final closure of the dike in 1932 to about 0.2‰ by 1938 where it has remained relatively constant up to the present.

A major portion of the landed fish catch prior to 1932 consisted of marine or euryhaline species, namely, eels (*Anguilla anguilla*), smelt (*Osmerus eperlanus*), and flounder (*Platichthys flesus*). Dike construction (initiated about 1919) must have exerted a stress on the fishery prior to final closure, however, by restricting movements of fishes from the North Sea into the Zuiderzee and perhaps restricting the movement of fishing vessels as well. A catastrophic decline in the fishery (Fig. 6) occurred between 1931 and 1933 (data supplied by J. Willemsen, The Netherlands), which was parallelled by a chlorinity reduction of from 6 to 3.3‰ and proceeding to a low of 0.2‰ by 1938. The lowest yields in the fishery occurred over this same period (1933–1938) when the environment was unstable and biotic limitations (osmotic and ionic) were unfavorable for both marine and primary freshwater species (Darlington 1957, p. 46). Brackish waters are known to be relatively depauperate and show a low species diversity compared with similar habitats in marine or fresh waters (Remane and Schlieper 1971). By 1938 the low of 0.2‰ chlorinity approached that described by Redeke (1933) for fresh waters, and primary freshwater species began to increase rather dramatically until a yield level

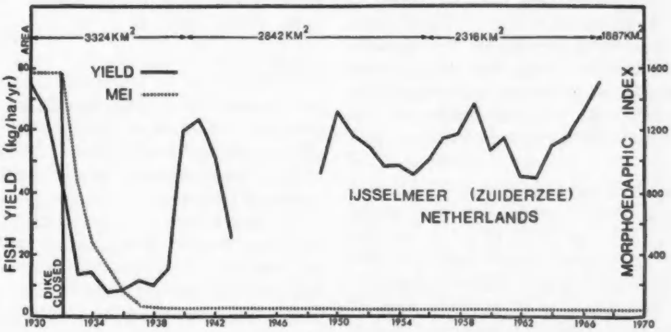


FIG. 6. Temporal changes in total fish yield and the morphoedaphic index with the closing of the dike which converted the marine environment of Zuiderzee into a freshwater lake (Ijsselmeer). The sequential reduction of area resulted from the creation of polders and was considered in the calculation of total fish yield per unit of area. Precise yield records were not available for the period 1944–1948.

close to 60 kg/ha was reached by 1940 (Fig. 6). At this time the landed catch was about equally divided between eels and freshwater species such as pikeperch (*Stizostedion lucioperca*), perch (*Perca fluviatilis*), bream (*Abramis brama*), and others. From 1940 until the present a mean yield of about 55 kg/ha has been maintained despite additional stresses on the system by the formation of reclaimed land (polders) which has drastically reduced the area of the Ijsselmeer to nearly half its original area.

The MEIs of both the Zuiderzee and Ijsselmeer were calculated for the period 1930–1967 by dividing the annual chlorinity level (assumed to be a correlate of TDS) by the mean depth (3.8 m). Physical stresses that caused the decline in the fishery prior to 1932 did not affect MEI levels until final closure of the dike that year. A drastic decline in the MEI from about 1600 to less than 500 occurred between 1932 and 1934 and parallelled the fishery decline for the period 1931–1933 (Fig. 6). Quite obviously, the MEI would not have been useful in predicting the extent of the fishery decline in this instance and a time lag of about 1 yr occurred between the response of the fishery to environmental changes and the indication of these changes by the MEI. The upsurge in the freshwater fishery responded rapidly, however, once the MEI reached its low of about 50 in 1938 and stabilized thereafter. Prediction of the 55 kg/ha mean yield level reached by the freshwater fishery alter 1940, was highly likely however if the Ijsselmeer were considered to be a temperate reservoir belonging to the family of reservoirs described by Jenkins (1967). In this case a MEI of 50 represented a standing crop of 200 kg/ha, which in turn could reasonably be expected to produce a mean annual yield of 55 kg/ha when exposed to an intensive fishery (assuming a yield of 0.4 × mortality × biomass (Gulland 1970). If a maximum yield equivalent to about one-third of the standing crop is assumed for a temperate zone fishery, then the 1967 high (75 kg/ha) may not be excessive but might tend to place undue stress on the most economically valuable species, usually the predators. Indeed, in recent years the landing of "nest" are dominant in the catch (J. Willemsen personal communication). ("Nest" consist primarily of pope (*Gymnocephalus cernua*) and small freshwater smelt, as well as a mixture of cyprinids and the immature of economically valuable species such as pikeperch and perch). Pikeperch may already be suffering the effects of harvesting younger year classes as a yield in excess of 3 kg/ha has not occurred since 1952 for that species although earlier yields on the order of 10 kg/ha of pikeperch were landed.

VOLTA RESERVOIR

The creation of an artificial lake usually results in an incomplete metamorphosis from the lotic to lentic environments. The transition period between first impoundment and ultimate water levels, with corresponding changes in nutrient concentrations, is an unstable period abiotically, and this instability is reflected biotically through the various species transformations. The Volta Reservoir, Ghana, provides a classic example of alteration of fauna and general biotic instability between the first stages of flooding in 1964 and the achievement of ultimate water levels in 1968 (Fig. 7). The former riverine population was dominated by various species of mormyrids (Petr 1969), but more recent information suggests that lacustrine species such as *Tilapia* sp., *Lates niloticus*, and several siluroids are by far the most abundant species, at least in total biomass.

During the period of increasing water levels and increasing nutrient levels (1964–1968) fish yields were overestimated by the MEI (Fig. 7), as the expansion of the ichthyomass could not maintain pace with the increased water volume and higher nutrient levels. This period was probably that of highest instability as species composition favored those few species preadapted to lentic living. Follwoing maximum water levels in 1968, however, the dynamic condition of the ichthyomass stabilized somewhat with the extinction of the abiotic depth variable, and biomass changes thenceforth depended primarily on changes in nutrient concentrations. From this point (1968), yield changes were completely predictable on the basis of the MEI 1 yr in advance of the actual harvest (Fig. 7). The MEI, then, between 1964 and 1968 predicted the potential yield possible had the reservoir been fully populated with lacustrine species able to take advantage of the increased nutrient levels and increased space. Following 1968, actual yield approached potential yield as the abiotic instability decreased and the MEI served as a useful forecast of future landed catch (Henderson et al. 1973).

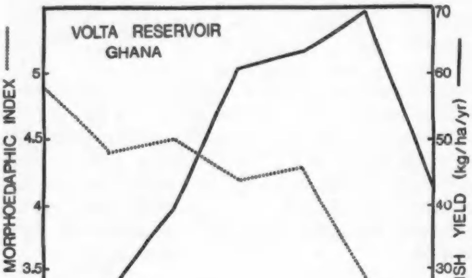


FIG. 7. Time-series plot of the total fish yield and the morphoedaphic index following closure of the impounding dam in the Volta Reservoir, 1964. In the first few years the MEI predicted the potential fish yield from the reservoir. However this was not achieved as the fish community had not yet responded to the limits of the rapidly expanding environment. In later years the MEI accurately depicted trends in fish yield about 1 yr in advance of the harvest.

LAKE ERIE

Three of the Laurentian Great Lakes have experienced substantial increases in TDS since 1900 (Beeton 1965). These changes have been attributed to cultural eutrophication and watershed modification resulting from massive human population increases in the watersheds of these lakes. TDS in Lake Erie has risen from 113 mg/liter in 1900 to about 200 mg/liter in 1970. MEI values have varied accordingly for the same period from 7.5 to 11.1. Total fish yield values, however, have remained approximately constant over the same time span (Regier 1973), an indication perhaps that even back in 1900 fishing pressure was sufficient to set into motion the various density-dependent compensating factors that tend to retain the homeostasis of the system. Starting with the species most adapted to oligotrophic conditions, several taxa have disappeared from the fisheries (Smith 1972; Regier 1973). The biotic hiatus vacated by these taxa has, however, been invaded by a new set of taxa which do not require oligotrophic conditions for their survival, growth, or reproduction. Some of these species have shorter life-spans and a higher natural mortality, which suggests that they have a greater yield potential than those species that formerly occurred in the lake and were adapted to oligotrophic conditions. That this higher yield potential was never reached is accounted for by two principal effects: (1) the lower economic importance of the replacement species (Regier 1973); (2) the loss of large areas of former fish habitat in the delta regions of tributary rivers (Smith 1972) and in the hypolimnion of the central basin (Carr 1962). The increase in MEI from 7.5 to 11.1 perhaps reflects adequately the increase in the potential yield of Lake Erie, if consideration is given to the loss of natural habitat through environmental degradation and the potential for increasing yield from available stocks. For example, if the economic climate were favorable for the harvest of large standing stocks of freshwater drum (*Aplodinotus grunniens*), the total fish yield of Lake Erie would be substantially increased. As it stands, however, the largest annual fish yields from Lake Erie occurred in the decades before and immediately after 1900 (Smith 1972), when the bulk of the catch consisted of high-value species (Baldwin and Saalfeld 1962), this despite technological improvements in fishing vessels and gear in later years. The MEI has therefore adequately represented the potential fish yield of Lake Erie since 1900, despite changes in its nutrient component over a period of about 70 yr.

LAKE ONTARIO

Increases in TDS levels for Lake Ontario have closely coincided with those for Lake Erie (Beeton 1965), its major source of affluent water. Additionally, Lake Ontario derives supplemental nutrients from cultural eutrophication within its own watershed (Christie 1972). If we consider the outer deep basin of Lake Ontario ($\bar{z}$ = 81 m) and the Bay of Quinte ($\bar{z}$ = 7.2 m) as contiguous components of the same aquatic ecosystem, or even as two subsystems linked by a water passage, then we may concern ourselves with the divergent effects of nutrient loading on the fisheries communities of each subsystem and the relative changes of MEI effected. Similarly we may contrast the changes of the fish communities in Lake Ontario with changes in Lake Erie as summarized by Christie (1973), Regier (1973), and Smith (1972).

TDS levels for Lake Ontario have increased for the period 1900–1960, from about 140 to 200 mg/liter (Beeton 1965) and corresponding changes in MEI for the Bay of Quinte were 19.4–27.8, and for the outer basin of Lake Ontario 1.7–2.5. Hence the absolute increase in the MEI of the Bay of Quinte (+8.4) was an order of magnitude greater than that of the main basin of Lake Ontario (+0.8). These relatively large differences in MEI increase between the two basins from a corresponding increase in TDS can be attributed principally to depth differences between the bay and the main basin. Furthermore, we have conservatively minimized these differences by considering a constant TDS increase in both basins. Preliminary studies in the Bay of Quinte (Hurley 1970) would suggest that increases in TDS, as indicated by conductivity measurements, were even greater there than in the outer basin of Lake Ontario as recorded by Beeton (1965).

Fish communities in the deep outer basin of Lake Ontario and the Bay of Quinte generally responded according to absolute changes in the MEI, although it may be impossible to document this on a relative production basis, as most of the new species inhabiting both basins are presently uneconomic (or at least less economic) to the commercial operators and catch records suffer accordingly. During a period of about 100 yr, the open lake populations of lake trout (*Salvelinus namaycush*), lake whitefish (*Coregonus clupeaformis*), and ciscoes (*Coregonus* sp.) disappeared (Christie 1972), leaving the lake populated with alewife (*Alosa pseudoharengus*) and rainbow smelt (*Osmerus mordax*). Coincidentally, burbot (*Lota lota*) declined to insignificant levels and the fourhorn sculpin (*Myoxocephalus quadricornis*) disappeared in recent years (Wells 1969); the latter species has never been commercially exploited and is the only known benthic feeder inhabiting the abyssal depths of Lake Ontario (Dymond et al. 1929). The lake trout, lake whitefish, burbot, and some of the deepwater ciscoes are dependent also on the benthic zone for at least part of their life histories, whereas the invading alewife and rainbow smelt tend to occupy the limnetic waters for the most part. It may be inferred that increased nutrients in the main basin of Lake Ontario have in some manner reduced the habitability of the deep benthic zone for fishes or their invertebrate food organisms, although perhaps not yet to the same extent as recorded in the central basin of Lake Erie (Carr 1962). The large volume of hypolimnion in the main basin may have diluted the effects of nutrient loading to some degree and oxygen deficiencies may not yet be a reality, yet almost certainly organic buildup of the bottom sediments has effected some physical and chemical changes with corresponding biotic reaction. It is possible that these changes have affected, in turn, benthic fish communities in a negative direction, while nutrient loading in the surface waters (euphotic zone) has enhanced the potential productivity of the alewife and rainbow smelt, two species with a lower trophic status than the extinct benthic predators, and therefore better able to take opportunistic advantage of the current nutrient regime. The apparent increase of potential productivity of the main basin as indicated by the MEI may, therefore, be a real one, but cannot yet be supported in terms of increased yield to the commercial fishery which is presently uneconomic except in the limited inshore areas (Christie 1973).

The shallow Bay of Quinte, on the other hand, has maintained its conglomerate of largely warmwater species, at least until recent years. Its per-hectare yield to the commercial fishery has averaged about an order of magnitude greater than that of the main basin of Lake Ontario. Another notable perturbation in the Bay of Quinte was the invasion of the white perch, *Morone americana* (Scott and Christie 1963), which had marked influence on the fish communities (Christie 1973). Some of the warmwater species such as white sucker (*Catostomus catostomus*), walleye (*Stizostedion vitreum*), and smallmouth bass (*Micropterus dolomieui*) decreased conspicuously following the incursion of the white perch into the bay, although the interactive effect is not known. However, low capture frequencies of other species such as northern pike (*Esox lucius*), bowfin (*Amia calva*), muskellunge (*Esox maskinongy*), largemouth bass (*Micropterus salmoides*), and longnose gar (*Lepisosteus osseus*), all large piscivores, were caused by events predating the white perch invasion (Christie 1973). It is probably sufficient to note at this stage that the Bay of Quinte over the past 100 yr has been subjected to several perturbations including nutrient loading and has undergone a series of complex and interactive changes in its fish communities which have not yet stabilized. Sorting out the individual stress effects on the various components of the fish populations is beyond the scope of this paper, however despite these various changes in abiotic parameters, including oxygen-deficient bottom waters (Hurley personal communication), there is no indication of an overall decrease in the productive capacity of the Bay of Quinte. As with Lake Erie, the per-unit-area productive capacity may actually have increased as indicated by the MEI increase. In this respect, the series of events experienced in the Bay of Quinte is more similar to those undergone in Lake Erie than to those in the deep outer basin of Lake Ontario. It is suspected that nutrient loading in particular is more effective in contributing to the loss of benthic animal communities in oligotrophic lakes, where in the large and cold hypolimnions there is insufficient heat and light energy to accommodate the increased nutrient load and thereby transform it into productive plant and animal matter. Shallow waters on the other hand, are more likely to be biologically accommodated, and increased nutrients are rapidly taken up in the organic sector of the ecosystem. It seems apparent that these differences are implicitly reflected by the MEI.

Implications for Ecological Theory

The power function relation between average fish yield and the MEI constitutes, as do various related models of similar form, an "ecological system model." That is, despite its extreme simplicity and undoubted mathematical shortcomings, the model expresses a dynamical system property in terms of state parameters that are common to all lentic ecosystems. On the basis of evidence reviewed earlier in this paper, the model adequately forecasts yield statistics for a variety of fisheries, of varying species composition, among a set of differing climatic regimes. Perhaps the model does so because of its very simplicity, hence great generality.

Power function relations are common in biology, and are perhaps best known from the classical work of Huxley (1932) on growth allometry. The power function is the simplest description of the constancy of increase of one variable relative to that of another.

It is consistent with current views of lake succession to observe that lake ensembles can in some ways reflect what is thought to be the normal time sequence of events in individual lakes. Introduction of a time dimension suggests a possible analogy between the MEI model and the familiar equation for allometric growth. Allometry of the MEI model would assert that the MEI parameters and fish yield both change with lake succession according to comparable rate functions. By this reasoning the power index of the model itself represents a ratio of the individual rate constants for the yield and for the MEI rate functions (see Rosen 1967). Accordingly, an interesting aspect of the MEI model is its possible "ergodicity" (equivalence of ensemble and time-series averages), in a very inexact sense of the term.

Of equal note is the implicit independence of the MEI model from the species composition of lentic food webs. The typological point of view is deeply rooted in post-Linnaean biology, and modern limnology reflects this influence. It is therefore worth remarking that the MEI is one of a relatively small set of ecological models that is independent of the typological paradigm. Independence from species composition, together with the ease with which the appropriate parameters can be measured, provide the principal elements of generality and utility in the model.

Finally, and perhaps most important, is the suggestion of biological conservatism implicit in the model. It appears that elaboration of yield is a relatively uniform property of fish production systems, contingent on a relatively few abiotic system parameters, and seemingly irrespective of trophic considerations (Kerr and Martin 1970). The question of system conservatisms, or uniformities, appears to be an important one in ecological theory (Dickie and Mann 1974; Kerr 1974; Goel et al. 1971). Detection and elucidation of system uniformities, such as the yield conservatism implicit in the MEI model, seems fundamental to the development of a robust theory of limnological processes.

We suggest, taken together, that at least three considerations of possible interest to theoretical ecology are implicit in the MEI model. These are: the apparent ergodicity of yield from fish production systems, the conservatism or uniformity apparent in such forecasts, and the nontypological nature of both of these phenomena.

Future Applications of the MEI

The implicit potential of the MEI has not yet been fully realized. Its present utilization has been restricted almost entirely to fish communities of moderate to high diversities in which compensating interactions among the various taxa tend to dampen marked fluctuations of individual species. As the MEI represents the inherent ability of a lake to absorb and recycle nutrients within its biotic components, it obviously has potential utility not only for the estimation of productive processes but also the inverse or destructive processes which lead towards eutrophication.

We may expect the MEI to be useful not only for estimating biomass or production of fish communities, but also of other biotic communities including all aquatic vertebrates, zooplankton, bottom fauna, macrophytes, phytoplankton, decomposers, or any other component of the living or nonliving biotic segment. The potential for doing so rests on the ability of future investigators to find suitable methods for measurement of these components, as well as the determination of correlates of TDS and mean depth that may be more suitable when related to them (e.g. Hargrave 1973). Additionally, the relative efficiency of relating the MEI to units of area or volume needs further study (see Brylinsky and Mann 1973) and perhaps relates to the inherent spatial requirements and behavior of the organism under consideration.

Perhaps the greatest immediate need of the MEI potential is for the estimation of standing stocks of marine organisms useful to man for future management of the resources of the sea. It would be not only instructive, but, hopefully, beneficial to make a potential yield prediction for the oceans of the world on the basis of the MEI that may be compared with those previously made from other sources (e.g. Ryther 1969; Gulland 1970). The MEI, although successfully applied to reservoirs (Jenkins 1967), has not yet been utilized for prediction of standing stocks of fishes in a reservoir still to be constructed (one such study is currently underway in Canada). More importantly, the MEI has the inherent ability of predicting accurately not only long-term asymptotic yield of fishes in these situations, but also peak yield during early filling stages (Henderson et al. 1973).

Neither has the potential use of the MEI in fish cultural operations been adequately explored. Predictions of future yield from a fish cultural station may determine the ultimate size of the station. Where the edaphic capability of the watershed and the morphometry of the future ponds are known, the potential for yield may be predicted by multiplying the MEI by a coefficient related to the relative feeding rate. When this information is compared with that for existing ponds, a prediction relative to the known yield from the latter may be made.

The MEI may also relate to production in terrestrial systems. If TDS adequately weights the proportional inputs of available soil nutrient, then yield of birds and mammals may be predicted in a general sense on this basis. Waterfowl in particular seem amenable to this type of treatment.

Finally, the MEI seems appropriately indicative of certain of man's environmentally destructive activities. As an indicator of biotic potential it holds promise as a useful prognosticator of the degree of development or human activity that should be allowed on a lake. On this basis, lakes or lake-groups may be zoned in the future for rational development of municipalities, summer resorts, cottages, or recreational uses, according to the innate qualities of a lake that allow a predictable amount of nutrient loading without altering either the physical, chemical, biotic, or aesthetic properties of the lake to a marked degree. Utilization of the MEI in this context, however, is dependent on future studies.

Acknowledgments

The concepts of the late D. S. Rawson provided the background necessary to prepare this paper and it is to him that it is gratefully dedicated.

Recent discussions or correspondence with E. K. Balon, M. Brylinsky, P. J. Colby, L. M. Dickie, F. E. J. Fry, H. F. Henderson, K. H. Mann, W. E. Ricker, and R. A. Vollenweider have provided further insights into the various subjects included in this paper, but we hold none of them responsible for our conclusions.

We gratefully acknowledge the following scientists who provided data, information, or analyses relevant to our study: J. M. Fraser, D. W. M. Hansen, B. T. Hargrave, D. W. Larson, N. V. Martin, J. M. MacMartin, J. Toivonen, R. Viitanen, and J. Willemsen.

K. K. Irizawa, J. K. McEwen, and R. Viitanen provided English translations of a Japanese, French, and Finnish paper, respectively.

Alexandrov, B. M. [ed.] 1959. The lakes of Karelia, their nature, the fish and fishing industry, a reference book. State Publishing House, Petrozavodsk, USSR. 619 p. (In Russian)

Alley, W. P., and C. F. Powers. 1970. Dry weight of the macrobenthos as an indicator of eutrophication of the Great Lakes, p. 595–600. *In* Proc. 13th Conf. Great Lakes Res.

American Public Health Association, American Water Works Association, and Water Pollution Control Federation. 1960. Standard methods for the examination of water and wastewater. 11th ed. New York, N.Y. 626 p.

Baldwin, N. S., and R. W. Saalfeld. 1962. Commercial fish production in the Great Lakes, 1867–1960. Great Lakes Fish. Comm. Tech. Rep. 3: 166 p.

Balon, E. K. 1972. Possible fish stock size assessment and available production survey as developed on Lake Kariba. Afr. J. Trop. Hydrobiol. Fish. 1: 45–73.

Beadle, L. C. 1969. Osmotic regulation and the adaption of freshwater animals to inland saline waters. Verh. Int. Ver. Limnol. 17: 421–429.

Beauchamp, R. S. A. 1939. Hydrology of Lake Tanganyika. Int. Rev. Hydrobiol. 39: 316–353.

Beeton, A. M. 1965. Eutrophication of the St. Lawrence Great Lakes. Limnol. Oceanogr. 10: 240–254.

Brylinsky, M., and K. H. Mann. 1973. An analysis of factors governing productivity in lakes and reservoirs. Limnol. Oceanogr. 18: 1–14.

Carlander, K. D. 1955. The standing crop of fish in lakes. J. Fish. Res. Board Can. 12: 543–570.

Carr, J. F. 1962. Dissolved oxygen in Lake Erie, past and present. Great Lakes Res. Div. Publ. No. 9: 1–28.

Christie, W. J. 1972. Lake Ontario: effects of exploitation, introductions, and eutrophication on the salmonid community. J. Fish. Res. Board Can. 29: 913–929.

1973. A review of the changes in the fish species composition of Lake Ontario. Great Lakes Fish. Comm. Tech. Rep. No. 23: 65 p.

Colby, P. J., G. R. Spangler, D. A. Hurley, and A. M. McCombie. 1972. Effects of eutrophication on salmonid communities in oligotrophic lakes. J. Fish. Res. Board Can. 29: 975–983.

Cordone, A. J., and T. C. Frantz. 1966. The Lake Tahoe sport fishery. Calif. Fish Game 52: 240–274.

Davis, C. C. 1955. The marine and freshwater plankton. Michigan State Univ. Press, East Lansing, Mich. 562 p.

Darlington, P. J. Jr. 1957. Zoogeography: the geographical distribution of animals. John Wiley and Sons, New York, N.Y. 675 p.

Dickie, L. M., and K. H. Mann. 1974. Aquatic ecological systems: the formal approach to holistic models. Ecology. (In press)

Dymond, J. R., J. L. Hart, and A. L. Pritchard. 1929. The fishes of the Canadian waters of Lake Ontario. Univ. Toronto Stud. Biol. Ser. No. 33: 1–35.

Fraser, J. M. 1972. Recovery of planted brook trout, splake, and rainbow trout from selected Ontario lakes. J. Fish. Res. Board Can. 29: 129–142.

Fonselius, S. H. 1970. Stagnant. Environment 12: 2–48.

Gibbs, R. J. 1970. Mechanisms controlling world water chemistry. Science 170: 1088–1090.

Goel, N. S., S. C. Maitra, and E. W. Montroll. 1971. On the Volterra and other nonlinear models of interacting populations. Rev. Mod. Phys. 43: 231–276.

Greenwood, P. H. 1958. The fishes of Uganda. The Uganda Society, Kampala, Uganda. 124 p.

Gresswell, R. K., and A. Huxley. 1965. Standard encyclopaedia of the world's rivers and lakes. G. P. Putnam's Sons, New York, N.Y. 384 p.

Gulland, J. A. 1970. The fish resources of the oceans. FAO Fish Tech. Pap. 97: 425 p.

Hargrave, B. T. 1973. Coupling carbon flow through some pelagic and benthic communities. J. Fish. Res. Board Can. 30: 1317–1326.

Harvey, H. H., and F. E. J. Fry. 1973. Sport fish index, p. 139–190. *In* The approach, theory, methodology and application of a lakeshore capacity model. Univ. Toronto, Environ. Sci. Publ. EG–10.

Hayes, F. R. 1949. The growth, general chemistry, and temperature relations of salmonid eggs. Q. Rev. Biol. 24: 281–308.

1957. On the variation in bottom fauna and fish yield in relation to trophic level and lake dimensions. J. Fish. Res. Board Can. 14: 1–32.

Hayes, F. R., and E. H. Anthony. 1964. Productive capacity of North American lakes as related to the quantity and the trophic level of fish, the lake dimensions, and the water chemistry. Trans. Am. Fish. Soc. 93: 53–57.

Henderson, H. F., R. A. Ryder, and A. W. Kudhongania. 1973. Assessing fishery potentials of lakes and reservoirs. J. Fish. Res. Board Can. 30: 2000–2009.

Hurley, D. A. 1970. Seasonal changes in several biotic and abiotic constituents at three stations in the Bay of Quinte. Ont. Dep. Lands For. Sect. Rep. (Fish.) 73: 50 p.

Hutchinson, G. E. 1957. A treatise on limnology. Vol. 1. Chapman and Hall, London. 1015 p.

Huxley, J. 1932. Problems of relative growth. 2nd ed. Dover Publications, New York, N.Y. 312 p.

Hynes, H. B. N. 1970. The ecology of running waters. Univ. Toronto Press, Toronto, Ont. 55 p.

Järnefelt, H. 1952. Limnological classification of lakes. Soc. Geogr. Fenn. 72: 202–208.

Jenkins, R. M. 1967. The influence of some environmental factors on standing crop and harvest of fishes in U.S. reservoirs, p. 298–321. *In* Proc. Reservoir Fisheries Symp., Southern Div. Am. Fish. Soc.

1970. The influence of engineering design and operation and other environmental factors on reservoir fishery resources. J. Am. Water Res. Assoc. 16: 110–119.

Jenkins, R. M., and D. I. Morais. 1971. Reservoir sport fishing effort and harvest in relation to environmental variables. Am. Fish. Soc. Spec. Publ. No. 8: 371–384.

Kemp, P. H. 1971. Chemistry of natural waters — VI. Classification of waters. Water Res. 5: 945–956.

Kerr, S. R. 1974. Structural analysis of aquatic communities. Porc. Its Int. Congr. Ecol. The Hague.

Kerr, S. R., and N. V. Martin. 1970. Trophic-dynamics of lake trout production systems, p. 365–376. *In* J. H. Steele [ed.] Marine food chains. Oliver and Boyd, Edinburgh.

Kozhov, M. 1963. Lake Baikal and its life. Dr W. Junk Publishers, The Hague. 344 p.

Larkin, P. A. 1964. Canadian lakes. Verh. Int. Ver. Limnol. 15: 76–90.

Larson, D. W., and J. R. Donaldson. 1970. Waldo Lake, Oregon: a special study. Oreg. State Univ. Water Resour. Res. Inst. WRRI-2: 21 p.

Loftus, K. H., and H. A. Regier. 1972. Introduction to the proceedings of the 1971 symposium on salmonid communities in oligotrophic lakes. J. Fish. Res. Board Can. 29: 613–616.

Lundbeck, J. 1934. Über den "primär oligotrophen" Seetypus und den Wollingster See als dessen mitteleuropäischen Vertreter. Arch. Hydrobiol. 27: 221–250.

Macan, T. T. 1963. Freshwater ecology. Longmans, London. 338 p.

Maloney, T. E., W. E. Miller, and T. Shiroyama. 1972. Algal responses to nutrient additions in natural waters. I. Laboratory assays. Limnol. Oceanogr. Spec. Symp. 1: 134–140.

Martin, N. V. 1955. Limnological and biological observations in the region of the Ungava or Chubb Crater, Province of Quebec. J. Fish. Res. Board Can. 12: 487–498.

1966. The significance of food habits in the biology, exploitation, and management of Algonquin Park, Ontario, lake trout. Trans. Am. Fish. Soc. 95: 415–422.

McCarraher, D. B. 1961. Sandhill lakes survey. A contribution of Federal Aid to Fisheries Restoration Proj., Job Completion Rep. F-4-P, 1954–1961: 83 p.

McPhail, J. D., and C. C. Lindsey. 1970. Freshwater fishes of northwestern Canada and Alaska. Bull. Fish. Res. Board Can. 173: 381 p.

Moyle, J. B. 1956. Relationship between the chemistry of Minnesota surface waters and wildlife management. J. Wildl. Manage. 20: 303–320.

Naumann, E. 1932. Grundzüge der regionalen Limnologie. Binnengewässer II: 196 p.

Neumann, J. 1959. Maximum depth and average depth of lakes. J. Fish. Res. Board Can. 16: 923–927.

Nickum, J. G. 1970. Limnology of winterkill lakes in South Dakota, p. 19–25. *In* A symposium on the management of midwestern winterkill lakes. Am. Fish. Soc. N. Cent. Div. Spec. Publ.

Northcote, T. G., and P. A. Larkin. 1956. Indices of productivity in British Columbia lakes. J. Fish. Res. Board Can. 13: 515–540.

Petr, T. 1969. Fish population changes in the Volta Lake over the period January 1965–September 1966, p. 220–234. *In* L. E. Obeng [ed.] Manmade lakes: the Accra Symposium. Ghana Univ., Press, Accra, Ghana.

Phillips, A. M. Jr. 1959. The known and possible role of minerals in trout nutrition and physiology. Trans. Am. Fish. Soc. 88: 133–135.

Poll, M. 1953. Exploration hydrobiologique du Lac Tanganika (1946–1947). Inst. R. Sci. Nat. Belg. III (5A): 251 p.

Pora, E. A. 1969. L'importance du facteur rhopique (équilibre ionique) pour la vie aquatique. Verh. Int. Ver. Limnol. 17: 970–986.

Powers, C. F., D. W. Schults, K. W. Malueg, R. M. Brice, and M. D. Schuldt. 1972. Algal responses to nutrient additions in natural waters. II. Field experiments. Limnol. Oceanogr. Spec. Symp. 2: 141–154.

Rawson, D. S. 1951. The total mineral content of lake waters. Ecology 32: 669–672.

1952. Mean depth and the fish production of large lakes. Ecology 33: 513–521.

1955. Morphometry as a dominant factor in the productivity of large lakes. Verh. Inst. Ver. Limnol. 12: 164–175.

1960. A limnological comparison of twelve large lakes in northern Saskatchewan. Limnol. Oceanogr. 5: 195–211.

Rawson, D. S., and J. E. Moore. 1944. The saline lakes of Saskatchewan. Can. J. Res. 22 (D): 141–201.

Redeke, H. C. 1933. Über den jetzigen Stand unserer Kenntnisse der Flora und Fauna des Brackwassers. Verh. Int. Ver. Limnol. 6: 46–61.

Regier, H. A. 1971. Evaluation of fisheries resources in African fresh waters. Afr. J. Trop. Hydrobiol. Fish. 1: 69–83.

1973. The sequence of exploitation of stocks in multi-species fisheries in the Laurentian Great Lakes. J. Fish. Res. Board Can. 30: 1992–1999.

Regier, H. A., A. J. Cordone, and R. A. Ryder. 1971. Total fish landings from fresh waters as a function of limnological variables, with special reference to lakes of east-central Africa. FAO Fish Stock Assess. Work. Pap. No. 3: 13 p.

Regier, H. A., and H. F. Henderson. 1973. Towards a board ecological model of fish communities and fisheries. Trans. Am. Fish. Soc. 102: 56–72.

Remane, A., and C. Schlieper. 1971. Biology of brackish water. John Wiley and Sons, New York, N.Y. 372 p.

Ricker, W. E. 1954. Stock and recruitment. J. Fish. Res. Board Can. 11: 559–623.

Ricker, W. E., and E. P. Weeks [ed.] 1973. FAO Technical Conference of Fishery Management and Development. J. Fish. Res. Board Can. 30: 1921–2537.

Rigler, F. H. 1964. The phosphorus fractions and the turnover time of inorganic phosphorus in different types of lakes. Limnol. Oceanogr. 9: 511–518.

Rodhe, W. 1949. The ionic composition of lake waters. Verh. Int. Ver. Limnol. 10: 377–386.

Rosen, R. 1967. Optimality principles in biology. Butterworths, London. 198 p.

Rounsefell, G. A. 1946. Fish production in lakes as a guide for estimating production in proposed reservoirs. Copeia 1: 29–40.

Ryder, R. A. 1961. Fisheries management in northern Ontario. Ont. Fish Wildl. Rev. 1: 13–19.

1964. Chemical characteristics of Ontario lakes as related to glacial history. Trans. Am. Fish. Soc. 93: 260–268.

1964a. Chemical characteristics of Ontario lakes with reference to a method for estimating fish production. Ont. Dep. Lands For. Sect. Rep. (Fish.) No. 48: 75 p.

1965. A method for estimating the potential fish production of north-temperate lakes. Trans. Am. Fish. Soc. 94: 214–218.

1970. Major advances in fisheries management in North American glacial lakes. Am. Fish. Soc. Spec. Publ. No. 7: 115–127.

1972. The limnology and fishes of oligotrophic glacial lakes in North America (about 1800 A.D.). J. Fish. Res. Board Can. 29: 617–628.

1973. Fish yield projections on the Nasser Reservoir — Arab Republic of Egypt. UNFAO Intern. Rep. 26 p. (mimeogr.)

Ryther, J. H. 1969. Photosynthesis and fish production in the sea. Science 166: 72–76.

Sanders, H. L. 1969. Benthic marine diversity and the stability–time hypothesis, p. 71–81. *In* Diversity and stability in ecological systems. Brookhaven Symp. Biol. No. 22.

Satomi, Y. 1962. The significance of alkalinity as an indicator of freshwater fish production. Inland Waters Mar. Res. Lab. Rep. 131, Freshwater Res. Rep. 12: 65–74. (In Japanese)

Schindler, D. W. 1971. A hypothesis to explain differences and similarities among lakes in the experimental lakes area, northwestern Ontario. J. Fish. Res. Board Can. 28: 295–301.

Schindler, D. W., F. A. J. Armstrong, S. K. Holmgren, and G. J. Brunskill. 1971. Eutrophication of Lake 227, experimental lakes area, northwestern Ontario by addition of phosphate and nitrate. J. Fish. Res. Board Can. 28: 1763–1782.

Schoenecker, W. 1970. Management of winterkill lakes in the Sandhill region of Nebraska. Am. Fish. Soc. N. Cent. Div. Spec. Publ. 53–56.

Scott, W. B., and W. J. Christie. 1963. The invasion of the lower Great Lakes by the white perch, *Roccus americanus* (Gmelin). J. Fish. Res. Board Can. 20: 1189–1195.

Sheldon, R. W., and S. R. Kerr. 1972. The population density of monsters in Loch Ness. Limnol. Oceanogr. 17: 796–798.

Sheldon, R. W., A. Prakash, and W. H. Sutcliffe Jr. 1972. The size distribution of particles in the ocean. Limnol. Oceanogr. 17: 327–340.

Smith, S. H. 1972. Destruction of the ecosystem in the Great Lakes and possibilities for its reconstruction. Univ. Wash. Publ. Fish. New Ser. 5: 41–46.

Stumm, W., and J. J. Morgan. 1970. Aquatic chemistry. Wiley-Interscience, Toronto, Ont. 583 p.

Sunde, L. A., J. Whitaker, and G. H. Lawler. 1970. Rainbow trout production in winterkill lakes. Am. Fish. Soc. N. Cent. Div. Spec. Publ. 57–63.

Viitanen, R. 1971. Helsingin läntisen merialeeun pohjaja rantaeläimistöstä. Vesiensuojelulab. Tied. No. 8: 90 p.

Vollenweider, R. A. 1968. Eutrofizzazione delle acque da fosforo. Riv. Ital. Sostanze Grasse 45: 99–107.

1969. Möglichkeiten und Grenzen elementarer Modelle der Stoffbilanz von Seen. Arch. Hydrobiol. 66: 1–36.

1970. Scientific fundamentals of the eutrophication of lakes and flowing waters, with particular reference to nitrogen and phosphorus as factors in eutrophication. Organ. Econ. Coop. Dev. Paris. 159 p.

Walters, C. J. 1971. Systems ecology: the systems approach and mathematical models in ecology, p. 276–292. E. P. Odum Fundamentals of ecology W. B. Saunders ,Toronto, Ont.

Watt, K. E. F. 1973. Principles of environmental science. McGraw-Hill, Toronto, Ont. 319 p.

Welcomme, R. L. 1972. Les eaux intérieures d'Afrique. UN/FAO/CIFA Tech Pap. 1: 117 p.

Wells, L. 1969. Fishery survey of U.S. waters of Lake Ontario, p. 51–57. *In* Limnological survey of Lake Ontario, 1964. Great Lakes Fish. Comm. Tech. Rep. 14.

Some Aspects of Great Lakes Physics of Importance to Biological and Chemical Processes[1]

F. M. Boyce

Department of the Environment, Water Management Service
Lakes Research Division
Canada Centre for Inland Waters, Burlington, Ont. L7R 4A6

Boyce, F. M. 1974. Some aspects of Great Lakes physics of importance to biological and chemical processes. J. Fish. Res. Board Can. 31: 689–730.

This is a discussion of some aspects of the physical behavior of the Great Lakes written for scientists with backgrounds in disciplines other than physics. The basic physical characteristics of Great Lakes basins are summarized. These characteristics are determined by the facts that (i) the basins are closed, (ii) the basins are large enough so that the Coriolis force is an important component of their dynamics, (iii) the principal source of mechanical energy is the wind, and (iv) the basins are vertically stratified in summer. Discussion of large-scale horizontal motions includes both currents and diffusion. The advection–diffusion equation is used as a framework for a discussion which includes a summary of the basic problem confronting hydrodynamic modellers, the parameterization of turbulence phenomena in terms of mean flow variables. Vertical transfer processes are considered, notably the measurement of vertical fluxes of heat and momentum and the computation of eddy diffusion coefficients, the prediction of thermal structure in terms of net surface wind stresses and heat fluxes, and the interactions of waves, currents, and turbulence in the thermocline. The dynamical structure of the coastal zone is outlined, and the review concludes with recommendations for future work on the understanding of vertical turbulent transports, the climatology of Great Lakes coastal zones, and an operational approach to verifying and improving numerical models of lake circulation.

Boyce, F. M. 1974. Some aspects of Great Lakes physics of importance to biological and chemical processes. J. Fish. Res. Board Can. 31: 689–730.

Cet article porte sur certains aspects du comportement physique des Grands lacs et s'adresse à des scientifiques dont la formation porte sur des disciplines autres que la physique. Nous résumons les caractéristiques physiques de base des bassins des Grands lacs. Ces caractéristiques sont fondées sur le fait que (i) les bassins sont fermés, (ii) les bassins sont suffisamment grands pour que la force de Coriolis soit un composant important de leur dynamique, (iii) la source principale d'énergie mécanique est le vent, et (iv) les bassins sont verticalement stratifiés en été. La discussion des mouvements horizontaux à grande échelle couvre à la fois les courants et la diffusion. Nous utilisons l'équation advection–diffusion comme cadre d'une discussion comportant un résumé du problème fondamental auquel ont à faire face les constructeurs de modèles dynamiques, l'établissement de paramètres pour les phénomènes de turbulence, en termes de variables de l'écoulement moyen. Nous examinons les processus de transfert vertical, en particulier la mesure des flux thermiques verticaux, et le momentum et le calcul des coefficients de diffusion tourbillonnaire, la prédiction de la structure thermique en termes de forces nettes exercées par le vent sur la surface et de flux thermiques, et enfin l'interaction des vagues, des courants et de la turbulence dans la thermocline. Nous donnons les grandes lignes de la structure dynamique des zones côtières. La revue se termine par des recommandations sur les travaux futurs visant à mieux comprendre les transports turbulents verticaux, la climatologie des zones côtières des Grands lacs et une méthode d'attaque opérationnelle dans le but de vérifier et d'améliorer les modèles numériques de la circulation des lacs.

Accepted January 31, 1974

---

[1] This paper, part of a special issue that comprises a comprehensive review of Limnology in Canada, was prepared to mark the 19th Congress of the International Association of Limnology (SIL), in Winnipeg, Man., during August 1974.

Printed in Canada (J3299)

The recent popularity of systems modelling as a research and management tool for components of the environment has stimulated a more unified approach to limnology, wherein biologists and chemists seek quantitative relations among input and output variables, and physicists turn from their traditional skirmishing on the least-guarded flanks of the enemy (Stommel 1970) to a more frontal attack on the understanding and ultimately the prediction of the physical state of lake systems in general. The fruits of this approach include much unsubstantiated wizardry and much disappointment in the face of the intractable complexities of nature, but will also include, where honest attempts are made, an invaluable faculty to any environmentalist, that of seeing things whole.

The aims of this review are two: first to summarize the current state of physical limnology in terms which we hope will be comprehensible to the nonphysicist, and second to outline some physical problems which we feel ought to be attacked in the near future. We shall deal in turn with the major characteristics of the Great Lakes basins, large-scale horizontal motions, the vertical transfers of energy, and the coastal zone, before giving our ideas on the most appropriate experiments for the future. We acknowledge the erudite review of physical limnology contributed by C. H. Mortimer at the 50 Year's Jubilee Symposium of the International Association of Limnology (C. H. Mortimer unpublished data), and we hope that this present review will complement it.

Before taking up the main themes of this work, we wish to draw attention to a particular bias common to fluid dynamicists. Unlike biologists trying to quantify basic relations among variables, the physicists already have a proven model at their disposal consisting of Newtonian mechanics of continuous media, as expressed by the Navier–Stokes equations.[2] In principle, deterministic predictions of the future states of a fluid in motion are possible, but in practice, the mathematical and computational difficulties of integrating the full set of equations are great. Much labor and ingenuity has been spent in seeking hypotheses and approximations which simplify the basic equations so that solutions may be obtained. There has been a historical tendency to find the approximate solutions first and then to look for the naturally occurring situation to which the solutions apply.

Thus the Navier–Stokes model, potentially of all-encompassing utility, is in reality like a pair of black-painted eyeglasses on which a number of scratches allow a fragmented partial vision. When a hydrodynamicist discusses a physical problem, he has in mind one of the many versions of the Navier–Stokes equations and must begin by describing the particular aperture (time and length scales of the phenomenon, for example) through which he now sees the world.

Various forms of this "aperture vision" appear throughout this discussion, and chiefly through the notion of scales. The Navier–Stokes model embodies the fundamental units of mass, length, and time. As we are discussing and comparing flows occurring in water, we are basically concerned with measures of length and time. For illustrative purposes, let us fix on flows occurring in a lake of length L, of width W, and mean depth H, such that $L > W > H$. Now L, W, and H could all serve as length scales depending on the phenomenon being studied. If the interest is in vertical exchange processes then an appropriate length scale is H, the mean depth of the lake. Vertical distributions of temperature, current velocities etc. will all run through their entire ranges of values in the interval $0 < z \leq -H$, where z is measured from the water surface and is taken to be positive in the upward direction. If we are studying diurnal changes in thermal structure, then an appropriate time scale is 24 h, as the effects produced by the changes will occur in intervals of time measured in small multiples of 24 h. Having chosen the basic scales of interest, we are now able to assess the relative importance of the various forces as they affect motions at these scales. Usually some forces are much more important than others, and we can simplify the basic equations of motion by neglecting the less important terms. Table 1 is a compilation of motions occurring in lakes and their associated length and time scales.

Basic Physical Characteristics of the Great Lakes

CLOSED BASINS

The Great Lakes constitute closed basins of generally simple configuration. Once introduced to

---

[2] The Navier–Stokes equations (see Batchelor 1967) are an expression of Newton's second law of motion, the balance of forces per unit mass and acceleration in each of three mutually orthogonal directions. The equations are derived in differential form and thus apply to an infinitesimally small volume of fluid. The forces include pressure force, gravitational force, Coriolis force, and viscous or friction forces. An equation of state for the fluid and an equation of continuity complement the three equations of motion and form a complete set of differential equations which may be solved in principle by integration over the volume of interest, taking into account the particular nature of the boundary conditions.

TABLE 1. Motions occurring in lakes. A partial list of lake motions and their associated time and space scales. Letters in parentheses refer to the nature of the scale used. M, amplitude of motion; S, distance over which phenomenon varies significantly; P, period; T, time interval over which phenomenon varies significantly; C, wave speed; V, vertical particle velocity; H, horizontal particle velocity. The governing terms in the equations of motion and continuity are listed in column 6 according to the code: 1, time-dependent horizontal accelerations; 2, time-dependent vertical accelerations; 3, advective component of horizontal acceleration; 4, advective component of vertical acceleration; 5, Coriolis force; 6, pressure gradient force due to slope of free surface, 7, pressure gradient force due to slope of the thermocline; 8, pressure gradient force due to atmospheric pressure field; 9, variations in bottom topography; 10, wind energy/stress; 11, internal stresses arising from horizontal current shear; 12, internal stresses arising from vertical current shear; 13, friction against lake boundaries; 14, potential energy changes due to surface heating and cooling.

(1) Phenomenon	(2) Length scale	(3)	(4) Time scale	(5) Velocity scale	(6) Dynamics major components	(7) Notes
	Horiz.	Vert.				
Wind driven surface gravitational waves	10 m(S)	1 m(M)	1S(P)	10 m/s(C) 1 m/s(V,H)	1,2,6,10	
Surface gravitational waves – seiches	100 km(S)	10 cm(M)	2–10 h(P)	2 cm/s(H)	1,6,9,10	
Short freely propagating internal waves	100 m(S)	2 m(M)	5 min(P)	2 cm/s(H)	11,2,7,10	
Long propagating internal waves steered by topography	10 km(S)	2 m(M)	1 day(T)	50 cm/s(C)	1,5,7,9,10	
Internal gravitational standing waves or seiches	10 km(S)	2 m(M)	16 h(P)	10 cm/s(H)	1,5,7,10	
Surface wind drift	–	10 cm(S)	-	2 cm/s(H)	10,12	
Coastal currents	10 km(S)	-	1 day(T)	10 cm/s(H)	all	Horizontal scale measured perpendicular to coast
Upwelling and downwelling	10 km(S)	10 m(M)	1 day(T)	<1 cm/s(V)	all	”
Wind driven horizontal circulation	100 km(S)	100 m(S)	1 day(T)	10 cm/s(H)	all	
Basin wide horizontal diffusion	100 km	-	1 mo(T)	-	all	Integrated effect of all motions
Langmuir circulations vertical mixing of epilimnion	–	10 m(S)	1 h(T)	1 cm/s(V)	1,2,3,4,10, 12,14, and others	Dynamics not yet understood
Formation and decay of thermocline	–	10–100 m(S)	1 mo(T)	–	10,12,14	

the basin, mechanical energy remains within the basin until its final dissipation and conversion to heat. Large-scale circulation pattern currents are strongly influenced by the bottom topography, and long gravitational waves tend to be reflected from the shorelines to form systems of standing waves within the basin. A contrasting situation would occur in an ocean of infinite horizontal extent. There, energy introduced to a finite zone would tend to spread outward through wave motions and viscous effects.

Physical Dimensions

Horizontal dimensions of the Great Lakes are small multiples of 100 km. Vertical dimensions are of the order of 100 m. The previous statement about containment of mechanical energy within the basin also implies a horizontal size small enough so that mechanical energy is distributed throughout the basin in a time interval short compared with the seasonal cycle (1 yr). The 1000-fold disparity between horizontal and vertical length scales means that significant vertical transfers of energy and materials take place in time intervals which are much less than the time required for significant horizontal mixing. On basin-wide scales, it can be shown that the ratio R

$$R = \frac{\text{Time taken for homogeneous vertical mixing}}{\text{Time taken for homogeneous horizontal mixing}}$$

is approximately

$$\frac{K_v L^2}{K_z H^2} \qquad (1)$$

where L and H are vertical and horizontal length scales, and K_z and K_v are vertical and horizontal eddy diffusion coefficients appropriate to the scales L and H (F. M. Boyce and P. F. Hamblin unpublished data) (Kullenberg et al. 1973). R ranges from $10^{-4}$to 10^{-2} for most Great Lakes situations.

The disparity between vertical and horizontal length scales encourages a mental separation of water movements into mainly horizontal and mainly vertical motions. One tends to think of the lake either as piecewise vertically-mixed basins which circulate horizontally, or as infinitely wide, horizontally uniform bodies of water which transfer energy and materials in the vertical direction only.

The horizontal dimensions of Great Lakes basins are sufficiently large that the apparent force due to the rotation of the earth as measured in coordinates fixed to the earth's surface (Coriolis force) has an important effect on the structure of currents and long-period waves. This force is proportional to the velocity of a fluid particle (constant of proportionality = f, the Coriolis parameter of dimension t^{-1}) and acts at right angles to the velocity. Free currents are deflected to the right, looking downstream in the northern hemisphere. In the Navier–Stokes model, the Coriolis force tends to couple north–south and east–west motions. Moreover, the strength of this coupling relative to other forces acting on the fluid depends on the time and space scales characteristic of the motions. Generally speaking, the longer the time scale of horizontal motion, the stronger the coupling.

The relative importance of Coriolis force in the dynamics of a particular phenomenon is determined by comparing the period or time scale of the phenomenon, τ, with the local inertial period, τ_I, which itself is a function of the Coriolis parameter, f. The simplest balance of forces involving the Coriolis force is one in which the water particles move horizontally in closed circles (clockwise in the northern hemisphere), with the centrifugal force being exactly balanced by the Coriolis force. If v is the speed of a particle and r is the radius of the circle it describes, then

$$\frac{v^2}{r} = fv$$

centrifugal force (outwards) = Coriolis force (inwards)

from which the period of its rotation works out to be

$$\tau_I = \frac{2\pi r}{v} = \frac{2\pi}{f}$$

This period is called the local inertial period, local, because the Coriolis parameter f, depends on latitude. In the Great Lakes region, f is essentially constant (10^{-4} s^{-1}) and τ_I is about 17.5 h. If τ is comparable to or greater than τ_I, the Coriolis force is usually important in the dynamics of the phenomenon in question. For example, a typical horizontal current speed in the lakes is 10 cm/s and a typical dimension of a Great Lakes basin is 100 km. A water particle travelling at this speed would take $\frac{100 \times 10^3}{0.1} = 10^6$ s to cross the lake. This is equivalent to 15 inertial periods, from which one concludes that the Coriolis force is important in the dynamics of basin-wide lake circulations.

MECHANICAL ENERGY INPUT FROM WIND

The principal source of mechanical energy to the lakes is the wind. The wind exerts a stress on the surface and transfers energy to the lake when the surface water is set in motion. A number of processes act to distribute this energy vertically through the water column. The structure of lake movements reflects strongly the input of mechanical energy at the surface.

A second major consequence of the wind's influence on the lake is the episodic nature of energy inputs to the lake stemming from the episodic nature of the winds themselves. Oort and Taylor (1969) specify a storm cycle through the Great Lakes of 2–7 days. As large lakes would take some time (many days) to adjust fully to a change in the winds from one steady condition to another, the state of motion at a given instant is the sum of remnants from earlier wind events plus the response to the winds of the moment. Only rarely is it possible (storm occurring after a long period of calm) to make a clear connection between cause and effect.

From a statistical point of view, the spectral analysis of long records of lake motions at a point (current speeds, water levels, thermocline displacements) show important energies at time scales which can be related to the passage of major wind events.

VERTICAL STRATIFICATION

In the summer months the Great Lakes exhibit the classical epilimnion-thermocline-hypolimnion thermal structure found in most deep lakes in the temperate zone. Some anomalies exist; in Lake Superior, periods of lake-wide stratification are short, in Lake Erie Central Basin, the hypolimnion tends to be thin and highly turbulent, presumably due to bottom friction (Burns and Ross 1972). By and large, the usual consequences of stratification, such as the effective sealing off of the hypolimnion from contact with the atmosphere and vertical diffusion barriers created by the thermocline region, operate also in the Great Lakes.

However, due principally to the size of the lakes, the stratification has a determining effect on large-scale horizontal motions. Roughly speaking, this effect occurs in two ways. In the open lake, one observes vertical oscillations of the thermocline coupled with rotary components of horizontal current having periods close to but less than the local inertial period. Mortimer (1971) has convincingly identified these motions as standing internal waves of lengths comparable to the basin dimensions. We shall often refer to these motions, but we direct the reader to Mortimer's own studies of the topic for a detailed explanation of their physics. The second manifestation of the effect of stratification on large-scale motion occurs in the nearshore or coastal zone of the lakes. Phenomena such as upwelling and downwelling, and episodic longshore currents occurring at time scales of several days, have their counterparts in the coastal zones of the oceans and can be explained in terms of complex interactions of friction forces, Coriolis forces, meteorological forces, and gravitational forces in which the stratification plays a determining role. We shall describe these nearshore motions in more detail below.

Large-Scale, Mainly Horizontal Motions in the Great Lakes: Currents and Diffusion

THE ADVECTION–DIFFUSION EQUATION, A FRAMEWORK FOR DISCUSSION

As our ultimate goal is the ability to understand and to predict the variations in time and space of the chemical and biological characteristics of a lake, it will be useful to set down an equation which describes mathematically the time rate of change at a point in the lake of a dissolved substance in terms of the water motions and sources of the substance. The usual procedure in deriving this equation is to imagine a rectangular test volume of water surrounding the point and to compute the net flow of the substance into this volume and the net amount of the substance generated within the volume by the sources. We must consider what we mean in practical terms by a point in a lake and an instant in time; in other words, we must define the time and space scales of interest. The choice is arbitrary and constrained only to the degree that the time and space scales are related. Suppose that we wish ultimately to describe the behavior of a nutrient substance in a lake basin over a period of weeks (spring algal bloom, for example). A "small" test volume in this context will then have horizontal dimensions of the order of a kilometer, vertical dimensions of the order of meters, and an "instant" in time would be a small portion of the diurnal cycle, say a few hours. We know that variations in the concentration field can be detected at much smaller time and space scales, but we assume, and the assumption is a big one, that the small-scale variability complicates but does not obscure the large-scale pattern. We shall return to this basic and important theme later.

Let s be the concentration (mass per unit volume) of the nutrient substance and let $\Delta x = \Delta y$ be the horizontal dimensions of the test volume and Δz be the vertical dimension of the test volume ($\Delta z << \Delta x$). Let U, V, and W be the components of current velocity in the two horizontal directions x, y, and the vertical direction z, respectively. Consider the net flux of nutrient into the test volume carried by the x component of current, when the central point of the test volume has coordinates x_o, y_o, z_o.

The orientation of the test volume is such that the positive x direction is east, the positive y direction is north, and the positive z direction is upwards. The x component of flux involves the east and west faces of the test volume defined by the planes

$x = x_o - \frac{\Delta x}{2}$ and $x = x_o + \frac{\Delta x}{2}$, respectively;

(net flux into test volume = time rate of change of mass of nutrient in the test volume due to x component of current) = flux through west face of test volume minus flux through east face of test volume

$$= (\overline{U\bar{s}})_{\left(x_o - \frac{\Delta x}{2}\right)} \Delta y \Delta z - (\overline{U\bar{s}})_{\left(x_o + \frac{\Delta x}{2}\right)} \Delta y \Delta z \qquad (2)$$

Similar expressions can be written for the net fluxes due to current in the y and z directions, and assuming that the test volume is small in the sense of differential calculus we may summarize the above expressions in calculus notation

$$\frac{\partial s}{\partial t} \text{ advective} = \frac{-\partial(\mathrm{U}s)}{\partial x} - \frac{\partial(\mathrm{V}s)}{\partial y} - \frac{\partial(\mathrm{W}s)}{\partial z} \qquad (3)$$

where both sides of expressions such as (2) have been divided by the volume of the test element Δx Δy Δz. (3) is defined formally by letting the test volume shrink to zero about the central point x_o, y_o, z_o. The left-hand side of (3) represents the portion of the total time derivative of s due to the advective component of net flux, that is to say the component due to the transport of nutrient due to the current field.

We shall consider next the diffusive flux which, in the context of a finite test volume and finite time and space scales, means the component of flux at time and space scales smaller than the scales of interest. These scales range all the way down to random molecular motion and by analogy with the latter, we assume that they are random in nature and that the flux due to them is proportional to the negative of the spatial gradients of the concentration field at the scale of interest. This analogy assumes in effect, that the diffusion process involves the random motions of finite-sized lumps of fluid as opposed to the random motions of molecules. The coefficient of proportionality is an eddy diffusion coefficient also appropriate to the scale of interest. Thus the expression for the net x component of diffusive flux is written

net flux into test volume = time rate of change of mass of nutrient in test volume due to diffusive flux in the x direction

$$= -(\mathrm{K}_x \frac{\partial s}{\partial x})_{\left(x_o - \frac{\Delta x}{2}\right)} \Delta y \Delta z + (\mathrm{K}_x \frac{\partial s}{\partial x})_{\left(x_o + \frac{\Delta y}{2}\right)} \Delta y \Delta z \qquad (4)$$

The net diffusive flux per unit volume including all directions is then written

$$\frac{\partial s}{\partial t} \text{ diffusive} = \frac{\partial}{\partial x}\left(\mathrm{K}_x \frac{\partial s}{\partial x}\right) + \frac{\partial}{\partial y}\left(\mathrm{K}_y \frac{\partial s}{\partial y}\right) \qquad (5)$$

$$+ \frac{\partial}{\partial_z}\left(\mathrm{K}_z \frac{\partial s}{\partial_z}\right)$$

where the eddy diffusion coefficients are assumed to depend on space and time (not necessarily constant).

Finally, there remains one additional component of the total time rate of change of s, that due to possible sources of nutrient. The sources may include transfers from the lake boundaries (sediments, atmosphere) when the test volume includes portions of these surfaces, and can also represent biological and chemical reactions of the most general kind. Formally we write

$$\frac{\partial s}{\partial t} \text{ source} = \mathrm{F} \qquad (6)$$

With the exception of fluxes across the lake boundaries, the specification of F in terms of s itself and other significant independent variables is the task of chemists and biologists.

The total time rate of change of s is now written

$$\frac{\partial s}{\partial t} = \frac{\partial s}{\partial t} \text{ advective} + \frac{\partial s}{\partial t} \text{ diffusive} + \frac{\partial s}{\partial t} \qquad (7)$$

$$\text{source} = -\frac{\partial(\mathrm{U}s)}{\partial x} - \frac{\partial(\mathrm{V}s)}{\partial y} - \frac{\partial(\mathrm{W}s)}{\partial z} +$$

$$\frac{\partial}{\partial x}\left(\mathrm{K}_x \frac{\partial s}{\partial x}\right) + \frac{\partial}{\partial y}\left(\mathrm{K}_y \frac{\partial s}{\partial y}\right) + \frac{\partial}{\partial z}\left(\mathrm{K}_z \frac{\partial s}{\partial z}\right) + \mathrm{F}$$

$$= \frac{\partial}{\partial x}\left(\mathrm{K}_x \frac{\partial s}{\partial x} - \mathrm{U}s\right) + \frac{\partial}{\partial y}\left(\mathrm{K}_y \frac{\partial s}{\partial y} - \mathrm{V}s\right)$$

$$+ \frac{\partial}{\partial z}\left(K_z \frac{\partial s}{\partial z} - Ws\right) + F$$

Alternatively, from the biological or chemical point of view, the interest may be centered in the production term, F, in which case (7) list the kinds of information needed to interpret field experiments designed to measure F. With the latter aim in mind, one could integrate (7) over the volume of the lake, thus removing any explicit dependence on the details of the velocity field or diffusion processes. The result is a budget equation for the substance over the entire lake, from which an average value of F could be determined.

Two things must be considered to decide on the validity of the lake-wide averaging approach. The first is the problem of sampling; enough properly spaced samples must be collected to obtain a useful average, and the time taken to collect the samples must be considered against the time scale at which one would like information on the process. The second problem arises when F is likely to be strongly dependent on the concentration s or other variable such as temperature, whose horizontal distribution may be nonuniform. If the functional dependence of F on this variable is other than linear, the actual dependence of F on s will not be related simply to the dependence of the average value of F on the average value of s.

Given the size of the Great Lakes basins and the variability of important physical, biological, and chemical characteristics, we shall have to deal explicitly with both the velocity field and the diffusion processes before some biological and chemical field experiments can be interpreted.

THE SEPARATION OF ADVECTIVE AND DIFFUSIVE TRANSPORTS: GEOPHYSICAL TURBULENCE

As we have suggested earlier, the distinction between advective transport and diffusive transport is arbitrary at all space scales except the molecular. At this scale, diffusion of a nutrient substance depends on the mobility of the dissolved ion or molecule and on the statistics of random molecular agitation, which is to say temperature, and not on the primary flow variables. At time and space scales pertaining to lakes, we must invariably talk about mean flow variables which vary significantly only over the time and space scales of interest, and the turbulent component of these flow variables which we assume to behave as random, unordered fluctuations characterized most significantly by a mean square value or variance, as the mean value of the turbulent component is by definition zero. In particular, the total variance of current fluctuations is written

$$E^1 = \overline{(u^1)^2} + \overline{(v^1)^2} + \overline{(w^1)^2}$$

where u^1, v^1, and w^1 are the fluctuating components of velocity, and the overbar denotes a time average over the time scale of interest. E^1 will be recognized as twice the kinetic energy per unit mass of the turbulent components of flow. The variance of the fluctuations can be compared with the square of typical values of the mean flow variable. For currents we define

$$E = U^2 + V^2 + W^2$$

which is twice the kinetic energy per unit mass of the mean flow.

For a particular choice of time and space scales the relative magnitudes of E and E^1 indicate the approach to be taken to equations such as (7). If $E > E^1$ then the advective terms will be important, if not dominant, and the parameterization of the diffusive fluxes via the eddy diffusion hypothesis may be a valid approach. If on the other hand $E < E^1$, as would be the case for mean flows averaged over several months, the advective terms in (7) are likely to be negligible compared with the diffusive terms. This case has been examined by F. M. Boyce and P. F. Hamblin (unpublished data) and will be discussed more fully below.

An estimate of E and E^1 for various choices of time scales may be obtained from long records of horizontal[3] currents (moored current meters). The time history of current speed is treated mathematically as the sum of infinitely many steady periodic components, from which an energy density function may be defined, $E(\sigma)$, where $E(\sigma)d\sigma$ is proportional to the kinetic energy of the components in the frequency range $\sigma - \frac{d\sigma}{2}$ to $\sigma + \frac{d\sigma}{2}$. The plot of $E(\sigma)$ versus σ is called the kinetic energy spectrum, and the area under the curve between two frequencies is proportional to the kinetic energy in that frequency band which is contained in the original current speed record. For Great Lake motions[4], the horizontal kinetic energy density function has a very small value near zero frequency and rises to a maximum somewhere between .003 and .005 cycles/hour (periods of 200-300 h). This maximum may be related to the passage of major wind events, and possibly to very long period rotating wave modes in lake basins (P. F. Hamblin unpublished data). Thereafter the plot of $E(\sigma)$ vs. σ slopes downward with increasing σ until the frequency associated with the local inertial period is encountered ($\tau_I = 17.5$ h; $\sigma_I = 0.057$ cycles/hour). In the band containing σ_I, the spectrum has a sharp local peak but the energy density does not attain values as high as the maximum at 200–300-h periods.

---

[3] The vertical component of motion is significant only at very small scales of motion.

[4] See Fig. 16 for an example of partial spectra computed from current meter records. The spectra are plotted on a log–log scale.

The peak at 17.5 h occurs because this period is a resonant period of water bodies the size of Great Lakes basins. This means that the coupling to the lake of energy contained in the driving forces within this band is particularly efficient. As one progresses to higher frequencies the curve of $E(\sigma)$ again slopes downward. Other peaks in the spectrum can be identified, but they are usually of minor importance compared with the 200–300-h peak and the 17.5-h peak. In the regions of the spectrum where $E(\sigma)$ is decreasing with increasing σ, the form of the curve is similar to the spectrum of turbulence produced by a constant mechanical agitation of a fluid at a particular frequency. In this case, the energy density is maximum at the forcing frequency and decreases at higher frequencies. The rate of decrease can be accounted for theoretically (Batchelor 1947) by considering that the turbulent eddies at low frequencies (and large space scales) generate further eddies at higher frequencies and smaller space scales, and so on until the eddy size becomes so small that viscous dissipation ultimately converts the energy into heat. Thus the complete lake energy spectrum can be interpreted as representing a turbulent cascade of energy from large to small eddies, with energy being injected into the system at essentially two frequencies (Ozimodov 1965) – the frequency associated with the passage of major storms, and the lake resonant frequency associated with the inertial period.

With the concept of the energy spectrum in mind, it is clearer why the division between advective and diffusive transports is arbitrary. The major time scale of interest constitutes a vertical dividing line on the spectrum plot; energy contained in the spectrum to the left of this line (lower frequencies) will be considered as that due to the large-scale motions which we wish to describe in detail, and energy contained in the spectrum to the right of this line (higher frequencies) will be considered as that due to small-scale or turbulent motions. For a detailed description of the large-scale motions to be meaningful in the sense of equation (7), the dividing line must be far enough towards the high frequency end of the spectrum so that the total energy of the large-scale motions is substantially greater than the total energy of the small-scale motions. It is clear from this picture that the parameterization of the small-scale motions is dependent on the choice of a principal time scale. As the eddy diffusion hypothesis is one of the most convenient, we must then allow for a variation of the eddy coefficients according to the principal time and space scales of interest. Generally speaking, the larger these scales, the larger must be the eddy coefficients to simulate the net effects of the small-scale motions.

At best, this intermingling of statistical properties of the flow field and deterministic calculations based on an idealization of the properties of continuous media (the Navier–Stokes equations) is an uneasy alliance. A full discussion of this topic is far beyond the scope of this paper, but it is central to the question of whether flows occurring in the oceans and atmospheres can be predicted in a deterministic way, and if so, for how long (Lorentz 1963).

LARGE-SCALE HORIZONTAL MOTIONS

General discussion — an example of aperture vision — The discussion of large-scale motions (those for which the dominant wavelengths, radii of curvature of streamlines, etc., are comparable to the overall dimensions of the basin) is a good example of "aperture vision" provided by solutions to suitably modified Navier–Stokes equations. These solutions or dynamical models, often extremely simple and restricted in application, have served as organizing concepts in the interpretation of otherwise confusing field data. Occasionally, as in the case of tidal theory, they have been remarkably successful tools of prediction. The discussion of this section is based on the results obtained from simple models. The results fit actual lake observations imperfectly, but well enough to support a few simplifying generalizations.

A model sufficiently simple to form a basis for a moderately realistic discussion is one which assumes piecewise uniform properties in the vertical, either as a single homogeneous water body or two homogeneous layers separated by a surface of discontinuity in density, a first approximation in a purely dynamic sense to the thermocline. The surface stress exerted by the wind is distributed uniformly through the surface homogeneous layer. The vertical balance of forces reduces to a hydrostatic balance; the pressure at any point is the weight per unit horizontal area of the water column above that point. One can imagine, in such a model, that individual water particles take the form of vertical prisms of constant volume but variable shape extending through the homogeneous layers. A prism taller than its neighbors tends to force the neighbors apart until all prisms have the same level (pressure forces), and lateral motion of one prism relative to its neighbors tends to drag the neighbors along with it (friction forces). The model represents a local balance among horizontal accelerations and forces due to wind stress, pressure, the earth's rotation, and usually crude simulations of lateral and bottom friction. Bottom topography of the lake is also included, because motion of a prism of fluid over an uneven bottom will induce changes in the pressure distribution which must be balanced by the other forces.

The types of response one sees through this aperture can be divided into two classes – wave-like motions and whole-basin circulations.

The simplest wave-like motions are the long, free surface waves, governed by similar dynamics as short, wind-generated waves. The principal ingredients in the wave dynamics are acceleration of the water particles and pressure gradients generated by displacement of the free surface and the force of gravity. The speed of these waves is $C_s = \sqrt{gH}$, where H is the local water depth. C_s represents the maximum speed at which elements of the lake's surface can readjust themselves to a change in the external forces. Taking the basin dimensions as L = 100 km, and a typical value of C_s as 30 m/s, the time scale of adjustment is $L/C_s = 1h$. Waves of sufficient length are reflected from the lake's lateral boundaries, and waves of appropriate periods are reflected back and forth within the basin, with incident and reflected wave adding together in such a way that at that period the whole lake participates in an organized mass oscillation (exchange between potential and kinetic energy) known as a seiche. The seiches are essentially mechanical resonances of the system, and the general theory of mechanical systems possessing resonant modes of motion shows that any unsteady energy input to the system excites the resonant modes more efficiently than other motions.

The second class of motion, the whole-basin circulations, is more simply visualized in a vertically homogeneous model in which we assume that the wind has blown steadily for a long time, so that the lake has fully adjusted to the applied exterior forces, and the resulting field of motion is everywhere constant in time. Although the surface wind stress may be uniform over the lake, the force per unit mass of water in the lake is inversely proportional to the depth of the water, as we assume, with some justification but at the expense of neglecting vertical variations in current profiles, that this force is now uniformly distributed through the water column. On the other hand, the net pressure force per unit mass due to surface or thermocline slopes does not depend on the depth of the fluid. This means that the balance among the wind-stress force, the Coriolis force, the pressure force, and the friction forces, must also vary from point to point in the lake, and consequently so must the velocity field (Fig. 1). Investigations of the solutions obtained for whole-basin circulations show that they are strongly dependent on bottom topography (Rao and Murty 1970). Setting-up such a field of motion in a Great Lakes basin takes some time, and estimates range from several days to several weeks, depending on the choice of parameters representing lateral and bottom friction (Simons 1971).

In a homogeneous lake, there is a clear separation between the time scales of the two types of response. This separation extends to the effect, from a biological point of view, of the motions on the redistribution of material within the lake; the free surface modes contain only a finite quantity of energy and produce only small and oscillatory particle displacements, whereas the whole-basin circulations are able to extract much larger amounts of energy from the wind and achieve a steady state only when friction losses equal wind power input, and when the circulation pattern everywhere represents a balance among Coriolis force, pressure force, and friction force. A true steady state situation is extremely unlikely, because the adjustment or set-up time scale is longer than the typical time interval between major wind events (Simons 1971). With each wind event, the lake responds with a fresh injection of energy to the free surface modes and a slow adjustment of the whole-basin circulations towards an equilibrium with the new wind-force distribution.

When the lake is stratified, the possibility of vertical displacements of the interface (thermocline) as well as those of the free surface, introduces an additional degree of freedom into both the wave-like motions and the whole-basin circulations. From a conceptual point of view, one can separate the response into one having the features of the response of a vertically homogeneous lake (barotropic mode) on which is superimposed a response governing the relative motion of one layer with respect to the other (baroclinic mode). The barotropic mode contains the free surface wave motions and whole-basin circulations much as before, whereas the baroclinic mode contains internal wave motions (gravity waves propagating on the thermocline) and whole-basin circulations involving shearing motion between the upper and lower layer. In any but the simplest constant depth models, these motions cannot be separated but must be studied as an integral whole, particularly as the wind-stress

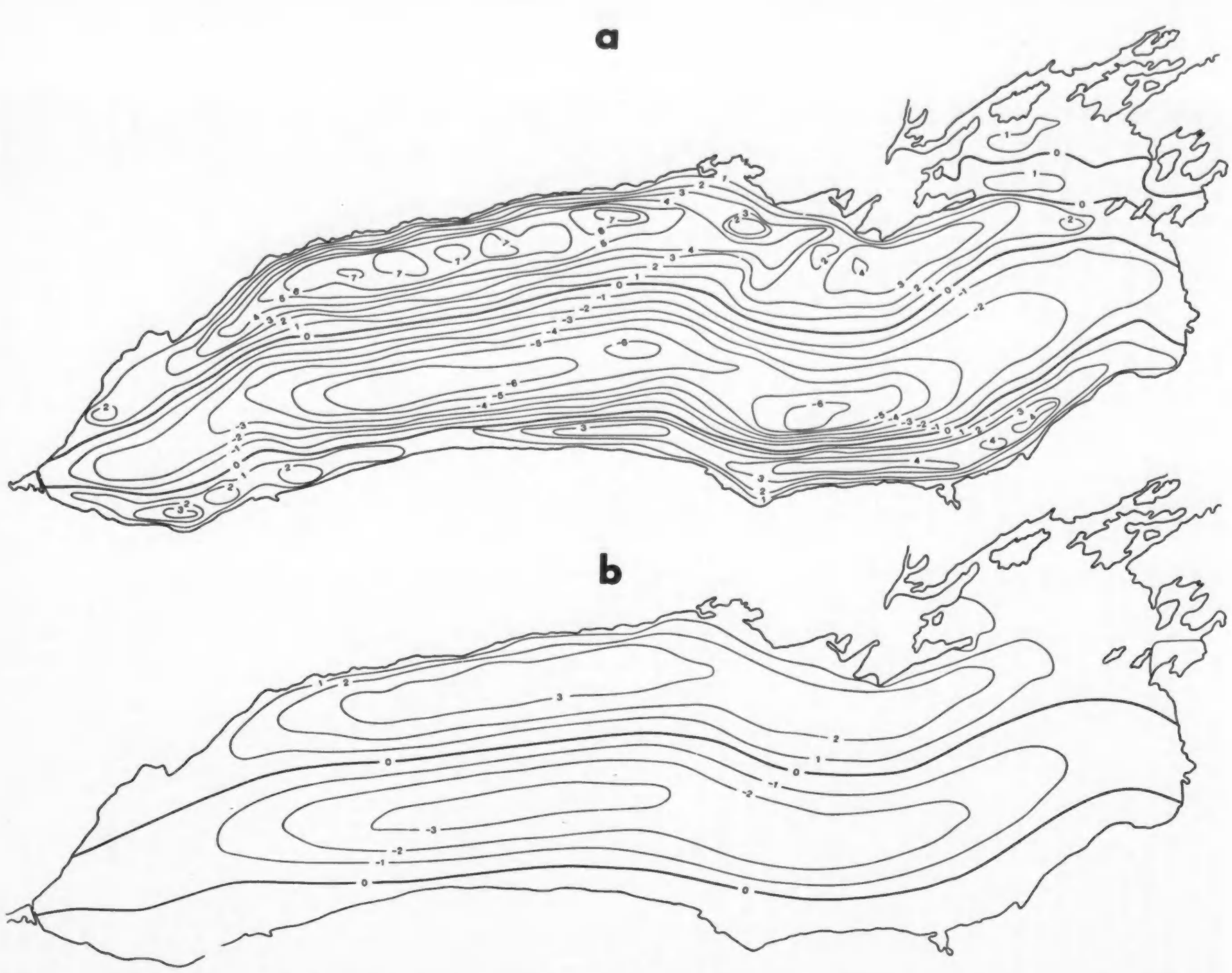


FIG. 1. a) (Simons 1971; his figure 8a) Eastward component of water transport after 2 days (approaching steady state) for an idealized westerly wind field following the passage of an atmospheric front. Contour lines are labelled in units of 1 m²/s. Coefficient of horizontal eddy diffusion, $K_r = 10^6$ cm²/s; bottom friction force taken to be proportional to transport and inversely proportional to water depth. Note the return flow in mid-lake (see Bennett 1973); b) (Simons 1971; his figure 8d) Same as Fig. 1a but with $K_r = 10^7$ cm²/s. Note the smoothing effect of an increased lateral diffusion coefficient.

force is now confined to the upper layer due to attenuation of vertical turbulence at the thermocline.

The velocity of long internal waves is about 1/50 to 1/100 that of surface waves, so that the adjustment time scale of interface slopes is of the order of 50–100 h or several days. Internal wave motions analogous to the free surface seiches exist in the Great Lakes, but their form is much more complicated due to the importance of the Coriolis force in the local balance of forces (Mortimer 1971). The separation of time scales between long internal wave motions and the fluctuations of wind-stress field is much less evident than in the case of surface gravity waves, so that one can expect internal wave motions to be a dominant feature of large-scale motions under stratified conditions. This is one of the salient features of the Great Lakes as compared with small stratified lakes and has important consequences regarding the vertical exchanges of energy and materials (Fig. 2).

For the Great Lakes basins, which are all much longer than they are wide, a simple model proposed by Bennett (1973) contains the essential ingredients for a first-order explanation of the transient response of the lakes to changing wind and in particular of dynamics of the coastal zone. The basic assumption is that the variation of the flow structure along the main axis of the lake is very small in comparison with the variation across the lake and may be neglected. This assumption is prompted by the elongated shape of the basins, by the speed with which the lake's free surface can adjust in response to changing wind stress, and by the relatively small displacements of water particles required to make this adjustment. The closed nature of the basins is reflected in mid-lake by the requirement that the net amount of water moved in the direction of the axis of the lake is zero, and that the cross-lake vertically averaged current is zero everywhere. These assumptions are supported by the success of simple wind set-up models which relate mean surface slope along the lake directly to the wind stress (Platzman 1963), and by the results of more complex numerical models (Simons 1971) which show little longshore variations of flow patterns in the central part of Lake Ontario. The effects of stratification are incorporated into this model by assuming the total fluid to be composed of two layers of slightly differing density.

The current-like total transport field, in response to a suddenly imposed wind stress acting along the lake, works out to be

$$Q = \frac{\tau_x}{\rho_0}\left(1 - \frac{H(y)}{\bar{H}}\right) t \qquad (8)$$

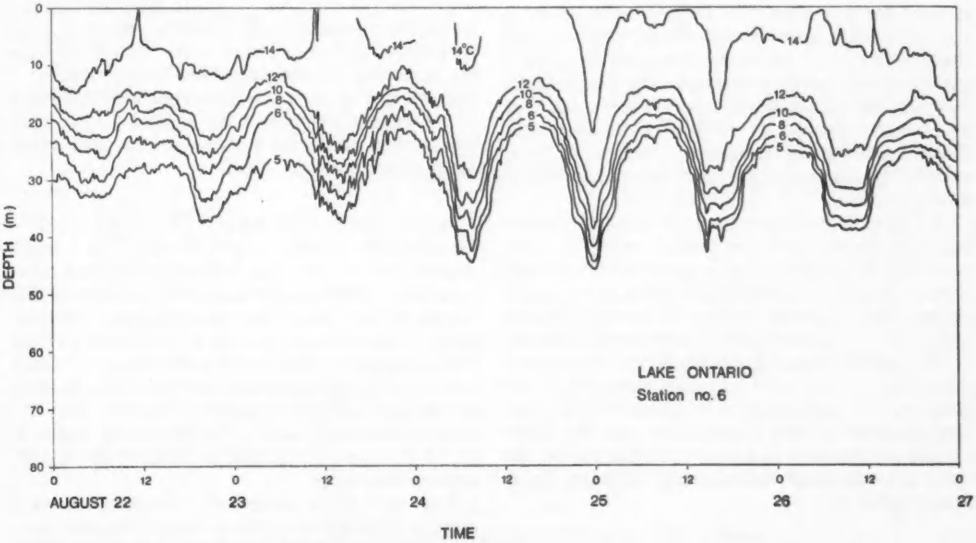


FIG. 2. A striking example of periodic vertical motion of the thermocline due to internal waves having periods near to the local inertial period. The measurements were made during September 1972, using a moored thermistor array (FTP). The location of the array is about 10 km offshore from Oshawa on the north shore of Lake Ontario (Station 6 [see Fig. 3] IFYGL mooring network). The plot shows isotherm depths as a function of time.

where τ_x is the wind stress along the main axis (x axis) of the lake,[5] $H(y)$ is the depth of the lake, expressed as a function of distance y, perpendicular to the main axis, and $\bar{H}$ is the mean depth of the cross section; t is the time measured from the instant the wind stress is applied. In a vertically homogeneous lake, Q is the product of the mean velocity component along the axis of the lake U, and the local depth $H(y)$. Thus an expression for U becomes

$$U = \frac{\tau_x}{H(y)\rho_0}\left(1 - \frac{H(y)}{\bar{H}}\right)t \qquad (9)$$

Both (8) and (9) show that the flow is the direction of the wind stress where the depth is less than the mean depth of the cross section, and opposite to the direction of the wind where the depth is greater than the mean depth. Furthermore, (9) shows, in the case of a homogeneous lake, that the flow velocity is largest near the shore becoming infinite as $H(y)$ tends to zero. Expression (9) is derived under the assumption that friction forces can be neglected. A more complete treatment including friction removes this singularity.

Note that the current-like component of total transport does not depend explicitly on the Coriolis force, but instead is determined by the wind stress and the bottom topography. This simple solution is valid for a limited time interval only, 10–20 h say, after the onset of the winds. Beyond that time, and after the winds die down, the circulation pattern almost certainly becomes more complicated. Nevertheless, equations (8) and (9) point out that the forced response to wind of a homogeneous Great Lake (or the barotropic component in a stratified lake) results in currents which are strongest near the coast.

The baroclinic component, in the case of a stratified lake, divides into two parts, a wave-like part consisting of cross-channel internal standing waves having periods somewhat less than the inertial period, and a current-like mode growing linearly with time. The current-like mode depends explicitly on the Coriolis force; facing downwind, the thermocline rises on the left-hand side (upwelling) and sinks on the right-hand side (downwelling). The displacements of the thermocline and the shear current between the two layers are greatest on the shore and decrease exponentially offshore, being proportional to

$$e^{-y/Y}$$

where y is distance from the shore and Y is the internal Rossby radius of deformation. Y is the distance a free internal wave would travel in 1/6 of an inertial period and is defined as

$$Y = \frac{c_i}{f}$$

where c_i is the speed of a long internal wave on the thermocline; c_i is about 25–50 cm/s under summer conditions, so that Y ranges from 2.5 to 5 km. The main part of the current-like baroclinic response thus is confined to within 5 km of the shore. When the two components, barotropic and baroclinic, are added together, the net result of stratification is seen to reduce the magnitude of vertical motion, to increase the width of the band of longshore current, and to introduce a shear between the upper and lower layers such that the speeds in the surface layer are increased and those in the lower layer are decreased.

The motion produced by a cross-channel wind stress consists of steady along-channel transport and standing wave motions. The current-like components of flow produced by the longshore component of wind outweigh any contribution by the cross-lake wind component after a few hours.

It is curious that the structure of the barotropic component of response is due to the fact that the free surface slope can adjust itself to the wind stress field in a small fraction of an inertial period, whereas the structure of the baroclinic component is a consequence of the comparatively slow adjustment of the interface slopes to the applied forces. Both components of the total response have their maximum effects near the coast.

A case history: the storm of 9 August, 1972 — Occasionally, a series of events allows us a much clearer view of the links between cause and effect in a lake's response to changing conditions. The August 9, 1972 storm on Lake Ontario came close to the ideal, occurring during an alert period of the IFYGL program and at the beginning of a multiship cross-lake temperature transect survey. Analysis of this data is still in progress but we can draw on some preliminary results for illustrative purposes (F. M. Boyce et al. unpublished data) (Staff C.C.I.W. unpublished data).

The wind stress computed from meteorological records obtained at stations 5 and 6 located on a line between Oshawa, Ontario, and Olcott, New York (Fig. 3 and 4) has a sharp peak centered on 1600 GMT August 9. The duration of the peak, the time interval for which the wind stresses are in

---

[5] $\frac{\tau_x}{\rho_0}$ has dimensions of velocity squared.

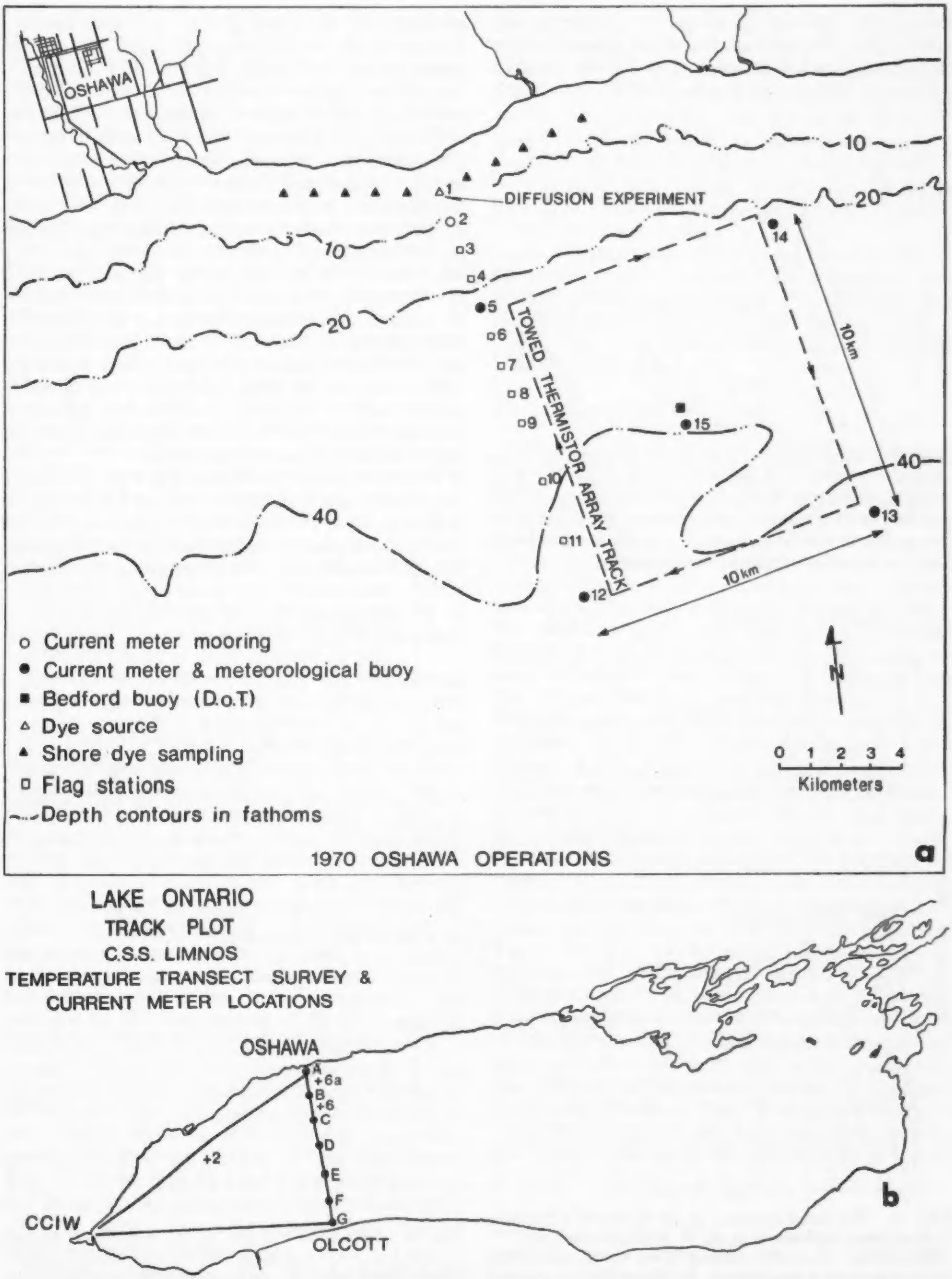

OSHAWA
DIFFUSION EXPERIMENT
10
20
40
1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
TOWED THERMISTOR ARRAY TRACK
10 km
10 km
N
○ Current meter mooring
● Current meter & meteorological buoy
■ Bedford buoy (D.o.T.)
△ Dye source
▲ Shore dye sampling
□ Flag stations
Depth contours in fathoms
0 1 2 3 4
Kilometers
1970 OSHAWA OPERATIONS
a
LAKE ONTARIO
TRACK PLOT
C.S.S. LIMNOS
TEMPERATURE TRANSECT SURVEY &
CURRENT METER LOCATIONS
OSHAWA
A
+6a
B
+6
C
D
E
F
G
+2
CCIW
OLCOTT
b

FIG. 3. Lake Ontario showing 1972 (b) transect line and locations of moored instruments 1970 (a) and 1972 (b) discussed in text.

excess of 1 dyn/cm^2, is about 12 h. During this interval the direction of the stress changed from east to southeast. The currents at station 6 and at station 6a (Fig. 5 and 6) measured at 10 m depth are presented after having been split into two frequency bands, a low-frequency band for periods longer than the inertial period (17.5 h) and a high-frequency band for periods comparable to the inertial period but longer than the periods of the free surface seiches. The low-frequency record at station 6 shows a sharp increase in current speed more or less in synchronization with the wind pulse during which the direction varies through 360°, but with a dominant southward component (clockwise rotation of the current vector). Thereafter the current moves eastward at varying speeds until about 1200 GMT on August 13, when a 180° shift in direction occurs. At station 6a inshore, (Fig. 6) the low-frequency record shows an increase in speed after the onset of the strong winds, with peak speeds occurring some 16 h after the peak wind stress. The direction of this current pulse is predominantly eastward, with a sudden 180° shift in direction occurring about 1200 GMT on August 12th.

From 0200 GMT on August 9 to 1407 on August 12, C.S.L. *Limnos* steamed back and forth across the lake along the Oshawa to Olcott line. Towed temperature profiling equipment was used to collect detailed information on the temperature structure

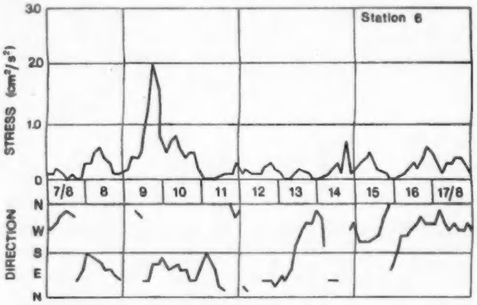


FIG. 4. Wind stress at Station 6 (see Fig. 3) from August 7, 1972 to August 17, 1972 (Staff C.C.I.W. unpublished data). Units of wind stress are expressed per unit mass of water. Nondimensional drag coefficient for winds at 4 m height is 1.2×10^{-3}, a value based on atmospheric turbulence measurements.

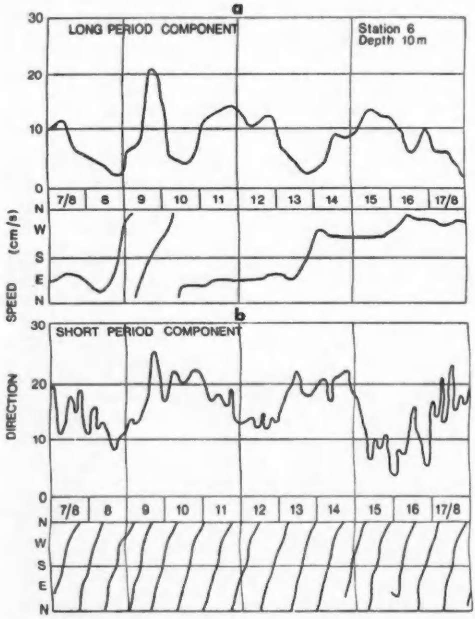


FIG. 5. Measured currents at 10 m depth a Sttation 6 (see Fig. 3) from August 7, 1972, to August 17, 1972. (Staff C.C.I.W. unpublished data). a) Long period current components; b) short period current components.

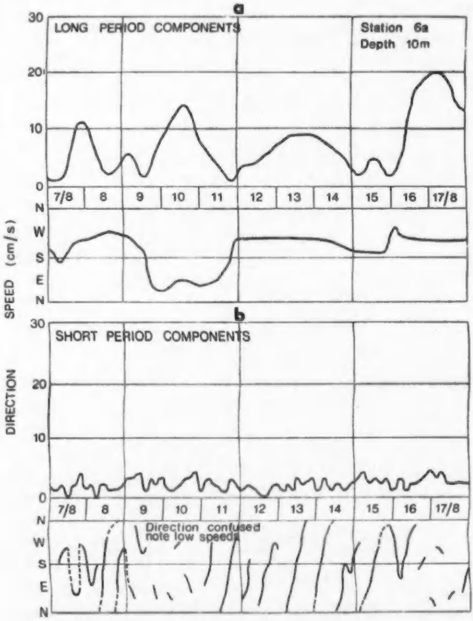


FIG. 6. Measured currents at 10 m depth at Station 6a (see Fig. 3) from August 7 to 17, 1972 (Staff C.C.I.W. unpublished data). a) Long period current components; b) short period current components.

down to 50 m depth. Each crossing took about 4 h. Data from three crossings, before the storm, immediately after the storm, and 30 h after the storm, (Fig. 8a–c) can be related to the long-period current meter records. The transect prior to the storm serves as a reference or initial condition (Fig. 7a). Points A and B approximately correspond to stations 6a and 6, respectively. Immediately after the storm (Fig. 7b) the surface temperatures have all decreased and the mean depth of the thermocline appears to have increased. This can be attributed to vertical mixing during the storm. The heat content at Point D (vertical integral of the temperature profile in mid-lake) has increased substantially; this can be correlated with the strong southerly component of surface flow at station 6 and the upwelling which appears to have taken place at point A. The marked dip in the thermocline between points E and F has been tentatively identified as a transient internal wave phenomenon (C. H. Mortimer and F. M. Boyce unpublished data). On the south shore the thermocline has deepened substantially and remains in this configuration for several days after the wind event (Fig. 7c). A more detailed examination of the regions between points E on the south shore suggests a frontal zone between two distinct water masses. The warmwater mass appears to be held against the south shore by the Coriolis force resulting from an easterly coastal current.

Turning to the high frequency band of current fluctuations, at station 6 (Fig. 5b) the current speed increases somewhat about the time of the storm, but is otherwise variable between 12 and 22 cm/s. The remarkable feature of this record is the regularity of the clockwise rotation of the current vector through 360° in about 17 h. From the continuity of these rotations before and after the wind event, it looks as though the timing of the wind pulse was in phase with an earlier series of rotations. This rotation of the current vector at or near the local inertial period can be explained in terms of our models, either as a purely horizontal motion to be expected far away from the shore (Pollard and Millard 1970) or as an internal gravity wave modified by both the rotation of the earth and the influence of the lake's boundaries (Mortimer 1971; Bennet 1973). A time series plot of isotherm depths at Point B (station 6) assembled from the series of transects (Fig. 8) shows vertical oscillations of the thermocline (10 C isotherm) of about a 17-h period, such that the instants of southerly current (Fig. 5b) in the high frequency band coincide with the crests of the oscillations of the thermocline after the storm. This data supports the idea of standing internal gravity waves.

Inshore at station 6a (Fig. 6b), it will be seen that the speeds of the high-frequency currents are much less than those encountered at 6a and the regular turning of the current vector is much less evident. The attenuation of the high-frequency components of current inshore during periods of stratification is an important feature of the lake's coastal zones and will be discussed below.

The above brief description of some observations of large-scale motion in the Great Lakes shows the type of data available and the complexity it presents to physical limnologists.

As the theoretical models suggest, we are able to distinguish between wave-like responses and aperiodic current-like phenomena. It is thanks to the insight provided by simple models that we are able to set this data, albeit tentatively, into a more general framework.

MEASURING THE VELOCITY FIELD

Our discussion of the advection–diffusion equation (7) as the framework within which chemical and biological processes must be considered, implies a necessity to measure the velocity field. The time variability of the currents at a point is usually such that a single instantaneous measurement of speed and direction can be considered as representative for only a short time, perhaps an hour at the most. The time variability and the space variability together can be dealt with only by using a dense array of moored current meters. If we fix on the idea of establishing a dynamic nutrient budget within a portion of the lake for the purpose of evaluating the reaction rate or uptake rate of the nutrient, it will be apparent that such experiments can meet only limited and well-defined objectives. Given that the mean value of current speed in the Great Lakes might be around 10 cm/s, or 10 km/day in round figures, an experiment designed to measure the diurnal variations in uptake ought to consider averaging over an area about 10 km on a side, (100 km^2) in order that the total flow through the area in a 24-h period should not entirely dominate the measurements. Although estimates would vary according to the location of the experiment (more dense array inshore), about 30 moored current meters and 5 fixed temperature profiles might provide a reasonable first order coverage of the epilimnion. This, needless to say, is a major undertaking, even as a purely physical experiment.

An alternative approach is the so-called Lagrangian[6] view, which would have the experiment follow

---

[6] The Eulerian view of fluid mechanics specifies the motion in terms of the components of the velocity field, u,v, and w, which are defined as functions of position and time

$$u = u(x,y,z,t) \text{ etc.}$$

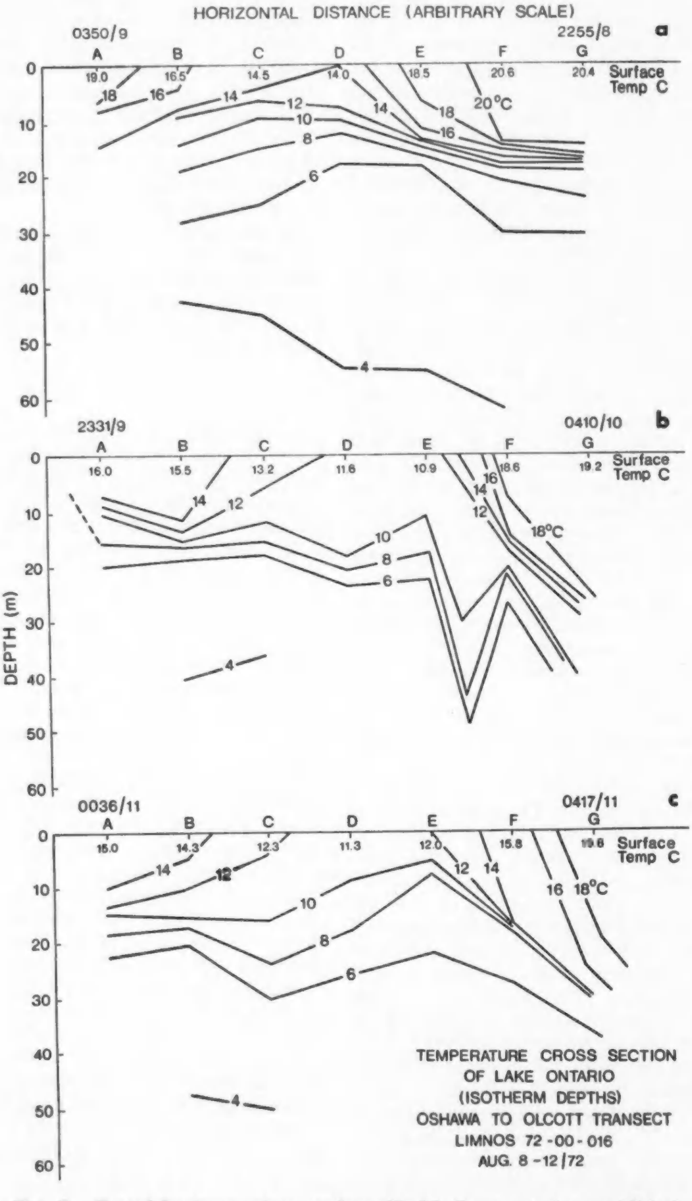


FIG. 7. Cross-lake temperature sections (F. M. Boyce et al. unpublished data) from *Limnos* transect cruise August 8–12, 1972. (see Fig. 3 for location) a) Section made prior to storm; b) section made immediately after storm; c) section made 30 h after peak of storm.

The Lagrangian view expresses the instantaneous position at time t of a fluid particle as a function of its initial coordinates, at $t = t_0$ and time

$$x_L = x_L(x_0, y_0, z_0, t).$$

a blob of water as it moved in the lake. In principle, this technique eliminates the need for explicit consideration of the velocity field although diffusive transports relative to the center of mass of the blob must still be considered and sampling over an area is required to determine concentration gradients. The problem with this technique is that of identifying the parcel of water to be followed. In principle, this can be done using drogues or marker dyes (if one can neglect the influence of the dye on the experiment). Time-averaging of experimental data would be necessary to remove effects of internal waves. The Lagrangian technique would be difficult in the coastal regions, due to the existence of strong and persistent horizontal velocity gradients, and so would lend itself best to open lake regions.

LARGE-SCALE HORIZONTAL DIFFUSION IN THE GREAT LAKES

Experimental determination of diffusion characteristics—By observing the spread of water-soluble dye on other tracer material in a lake, it is possible to estimate effective values of eddy diffusion coefficients. Murthy (1973) has summarized results of many experiments made in the epilimnion of Lake Ontario. A typical experiment starts with the introduction of a slug of water-soluble rhodamine dye into the epilimnion. The subsequent growth of the patch of dye is measured as a function of time from ships and launches equipped with continuous pumped sampling apparatus and fluorometers. Experiments have continued up to 60 h after the release of the dye, at which time the patch may have an effective diameter as large as 15 km.

In the early stages of an experiment, the shape of the dye patch is strongly modified by the local current field. There is a tendency for the patch to elongate in the direction of the mean flow and to take on a clockwise curvature in this direction, and

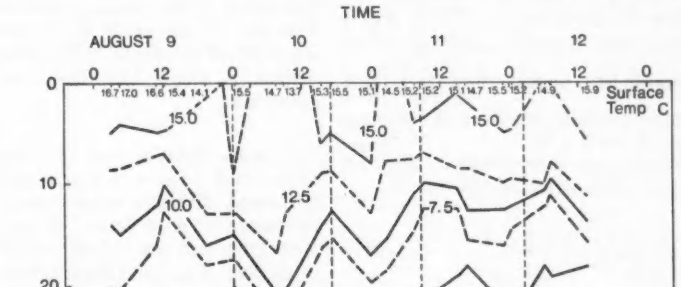


FIG. 8. Time series of temperature structure at point B (Station 6) constructed from *Limnos* transect cruise data (August 8–12, 1972). Dashed vertical lines are drawn at the times when the 10-m current (short period component) flows southwards. See Fig. 5b) at Station 6. This diagram reveals a definite phase relationship between currents and vertical motion of the thermocline which is indicative of internal standing waves (Mortimer 1971; Bennett 1973).

for dye concentrations to be higher in the leading edge of the cloud (Fig. 9). These features have been reported by other investigators (see Okubo 1971) and are related to observed tendencies for turbulent fluctuations in the direction of the mean flow to be more intense than those at right angles to it, and also to the "smearing" effects of vertical shear in the upper layer. When the patch has grown to the size of kilometers, the localized inhomogeneities in the mean flow field influence the growth of the patch to a lesser degree, and the horizontal diffusion process becomes much more symmetrical with respect to the centre of the patch.

The first stage of the analysis of the experiment is to compute the variance of the diffusing patch as a function of time, t. $t = 0$ corresponds to the instant of dye release. For a radially symmetric patch[7] the variance, $S^2(t)$, is defined

$$s_r^2(t) = \frac{\int_o^\infty r^2 C(r,t)\, 2\pi r\, dr}{\int_o^\infty C(r,t)\, 2\pi r\, dr} \tag{10}$$

where r is the radius measured from the center of the patch and $C(r,t)$ is the vertically averaged concentration of dye. If the dye were uniformly distributed in a circular area, of radius r, $S_r^2(t)$ would be equal to $\frac{r^2}{2}$, and is thus a measure of the size of the patch or more precisely, the area of the zone containing most of the dye.

From the variance, an eddy diffusivity may be defined. For the circularly symmetrical case

$$K_r = \frac{S_r^2(t)}{4t} \tag{11}$$

This definition arises from the solution of the horizontal diffusion equation with a constant diffusivity for the spread of a patch from an impulse discharge at a point. The variance of the dye distribution in this model at time t after the discharge is $4K_r t$, where K_r is the constant diffusivity. Thus the diffusivity defined by (11) is the one which would have to be invoked in a constant horizontal diffusion model to account for the variance observed at time t. A length scale of the diffusing patch can be defined from the square root of the variance (standard deviation)

$$l_r = \beta S_r,$$

where β is usually taken to be 3; l_r is representative of the size of the patch. When $K_r(t)$ is plotted against $l_r(t)$ on log–log paper, the experimental points group themselves about a straight line

$$K_r = 1.36 \times 10^{-3}\, l_r^{1.36} \tag{12}$$

Alternatively, K_r can be plotted against diffusion time, t. Similar results have been obtained for experiments conducted in the oceans (Okubo 1971).

Murthy (1973) points out that the above formula, although useful for modelling practical diffusion problems, is really only a statistical parameterization and does not explain the physics of the process. The next step would be to determine the relevant properties of the turbulence from direct measurements of the flow characteristics and then to relate these to effective diffusivities to establish how K_r depends on the governing environmental parameters.

C. R. Murthy et al. (unpublished data) report that similar results were obtained for horizontal diffusion within the thermocline and hypolimnion. Again K_r was proportional to the 4/3 power of the length scale, but the constant of proportionality was about 1/5 the value obtained in the epilimnion. This can be explained in a plausible fashion by arguing that the supply of turbulent energy to those regions is much less that the supply to the epilimnion.

A simple diffusion model for the offshore regions of the Great Lakes — A salient feature of large-scale horizontal diffusion experiments is the apparent tendency for "acceleration" of the diffusion process with time and size of the diffusing patch. The arguments of (p. 695) suggest why this must be so. In a closed basin of width W, this acceleration process must halt once the patch diameter becomes comparable to W. Clearly the size of the largest horizontal "eddy" must be less than W. F. M. Boyce and P. F. Hamblin (unpublished data) argue that at sufficiently large time and space scales, the horizontal transport of soluble materials within a Great Lakes basin can be viewed as a diffusion process alone, with the advective terms being contained in the diffusion terms. Moreover, such a process ought to be represented by a constant diffusivity characteristic of the largest "eddies" acting to transport the materials within the basin.

The distribution of chloride ion in the central basin of Lake Erie provides an excellent test case for the verification of such a model, both from the completeness of the field data and the particularly simple basin geometry, which can be approximated by a rectangular basin with constant depth. Data on sources of chloride ion to the basin (averaged

---

[7] Any arbitrary distribution can be analyzed as an equivalent radially symmetric distribution by replotting the contours of constant concentration as circles containing the same area.

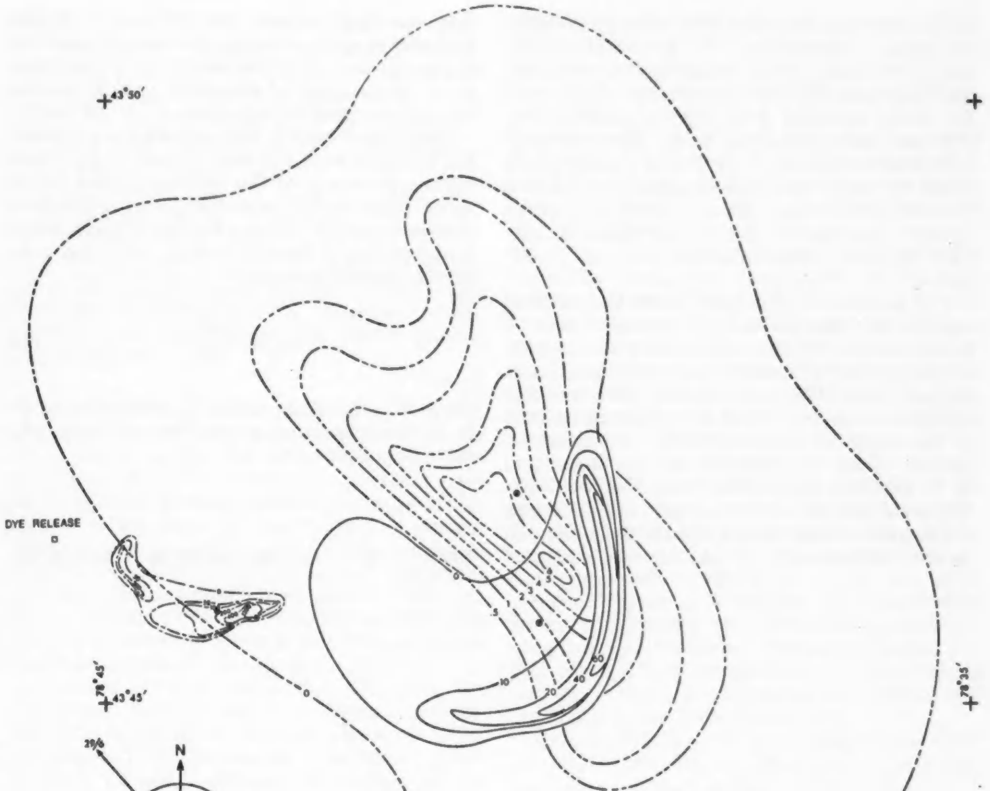

43°50′
DYE RELEASE
78°45′
43°43′
78°35′
0
.5
1
2
3
4
5
6
10
20
40
60
N
29/6
28/6
27/6
CURRENTS
SCALE: RADIUS = 10 CM/S
QUASI-SYNOPTIC HORIZONTAL DISTRIBUTION OF DYE CONCENTRATION IN FLUOROMETER UNITS, JUNE 27-29, 1972.
● DYE PATCH CENTER OF GRAVITY
▫ DYE RELEASED 1400Z 27/6/72
7 H AFTER RELEASE
26 H
53 H
1 0 1 2 3 4
KILOMETERS

FIG. 9. Quasi-synoptic horizontal distribution of dye concentrations (in fluorometer units) at 3 m depths and at different times after dye release. Expt E6, June 27, 1972 (Murthy 1973).

over a year) and on mean flow through the basin were used to compute the distribution of chloride ion in the basin and to estimate a value of K_r. The calculated distribution compares closely with the yearly averaged distribution assembled from 1970 monitor cruise data (N. M. Burns personal communication) (Fig. 11). Values of K_r were found which are within the expected range for a diffusing patch of conservative substance having a diameter equal to the width of the Central Basin of Lake Erie (80 km). These values are $2.0\text{–}2.5 \times 10^6$ cm^2/s.

The distribution of mercury in the sediments of Lake Ontario also seems to fit a version of the above model, wherein it is assumed that the rate of transfer of mercury to the sediments is proportional to its concentration in the water column above, and that this last concentration field can be calculated from a knowledge of the distribution of sources of mercury along the shoreline (F. M. Boyce and P. F. Hamblin unpublished data; Thomas 1972). The correspondence between model and prototype is less good in Lake Ontario than in Lake Erie, but then the true situation is much more complicated than the simple model. The diffusion coefficient necessary to account for the distribution of mercury in the sediments of the Western Basin of Lake Ontario is of the order of magnitude expected on the basis of the previous arguments (1×10^6 cm^2/s).

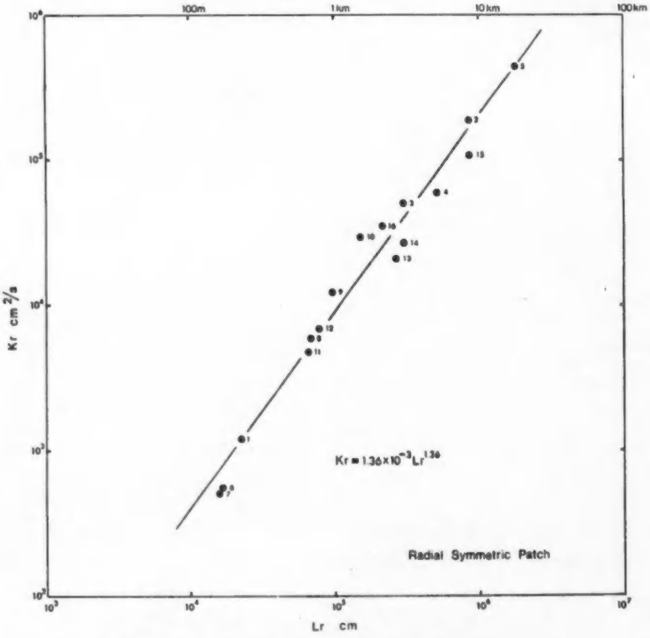
From these results two important conclusions can be drawn. First, the time required for significant horizontal mixing of the offshore regions of the Great Lakes is relatively short, ranging from one to several months. Using a Fickian diffusion model (constant K_r), a time interval for effectively complete horizontal mixing is

$$\tau_m = \frac{4W^2}{\pi^2 K_r} \qquad (13)$$

where W is the basin width. The best estimate for K_r is an extrapolation of equation (12). Using (12) and (13) we get

$$\tau_m = 2.9 \times 10^2 \ W^{0.64} \qquad (14)$$

where τ_m is in seconds and W is in centimeters.



EDDY DIFFUSIVITY VS LENGTH SCALE OF DIFFUSION

FIG. 10. A diffusion characteristic-eddy diffusivity vs. length scale of diffusion for a radially symmetric patch (Murthy 1973).

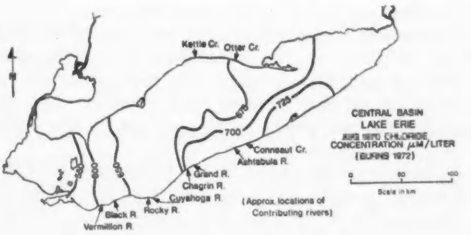


FIG. 11. Annually averaged distribution of chloride ion in the Central Basin of Lake Erie. 1970 monitor cruise data (F. M. Boyce and P. F. Hamblin unpublished data; data made available by Burns personal communication).

Second, since τ_m is comparable to or less than the period of stratification (τ_m <1 yr for all the Great Lakes basins), the offshore regions of the lakes are well-mixed horizontally; persistent horizontal gradients of conservative substances can be related to the shore line distribution of sources. Thus, from a biological point of view we expect that the processes occurring offshore are dominated by vertical exchanges of energy and materials, and from a practical point of view, a relatively small number of sampling points in the offshore regions ought to suffice to examine these processes.

Equation (7) and subsequent discussion has centered on the prediction of the mean concentration field averaged over the time and space scales of interest. From an environmental hazard point of view, we need additional information on the fluctuations in concentration about the mean. As an extreme example, we might argue that exposure to a predicted mean concentration of a toxic pollutant might be tolerated by an organism, whereas momentary exposure to a higher concentration (mean plus fluctuation) could be harmful. The risk of this kind of exposure can be stated only in probabilistic terms and to do this we need to determine the mean concentration, the standard deviation about the mean (expected magnitude of the fluctuations), and the form of the probability distribution of the fluctuations (Csanady 1973, chap. VII). The form of the probability distribution of concentration fluctuations poses difficult theoretical and experimental problems at the heart of which lies our present unsatisfactory knowledge of the structure of oceanic and lacustrine turbulence.

GETTING IT ALL TOGETHER: NUMERICAL MODELLING AS A RESEARCH TOOL

From the foregoing discussion, the rather pessimistic conclusion can be drawn that the collection of sufficient physical data to permit the unequivocal interpretation of large biological and chemical field experiments is an expensive and difficult task. The terrain for such pitched battles must be carefully chosen.

On the other hand, time series physical data of the kind examined on p. 700, current meter records, temperature profiles, and wind-stress measurements, themselves insufficient to define completely the physical environment as a function of time and space, serve as points of control against which theoretical models can be compared. As we have suggested, the simplest of models have contributed to a winnowing of ideas to the point that the important components of a general lake circulation model are fairly well understood. Moreover, it is generally admitted that a realistic model must necessarily depend on numerical computations made with a computer, if only because of the importance and the complexity of real-lake bottom topography. There are three main obstacles to the construction of a successful circulation model. The first is the great complexity of the computations required. The second is the correct parameterization of turbulent phenomena in terms of a small number of "mean" flow variables. The third obstacle is the predictability in a deterministic sense of phenomena operating in a continuum of space and time scales. These obstacles form a nested set, in that the second is a consequence of the third, and the first devolves from the second.

Simons (1971, 1972, 1973) has assembled powerful yet generalized tools for the systematic investigation of numerical models of lake circulation. Herein we shall briefly review Simon's work, as it is an excellent present-day guide from first principles to the frontiers of mathematical modelling of the physical behavior of lakes.

The basic equation of fluid mechanics can be written as conservation laws similar in form to equation (7). The quantity s is replaced by each of the horizontal components of velocity and density in turn, for a total of four equations, the last of which represents conservation of mass. The source term in equation (7) now includes pressure, gravitational, and Coriolis forces, where appropriate. The diffusive fluxes are expressed using the eddy diffusion hypothesis. Horziontal and vertical diffusion coefficients are then free parameters of the model. The mechanics of numerical modelling consist of the following steps:

(i) Define the volume of integration, i.e. the lake, as a three-dimensional stack of small-volume elements. This step determines the spatial resolution of the model and this choice effectively decides what is large-scale motion and what is turbulence. Several nested sets of volume elements may be needed. Usually the volume elements are defined by sets of intersecting planes, the lake surface (movable), and the lake bottom (fixed). The center of each volume element becomes a grid point.

(ii) Choose an appropriate finite-difference form of the conservation equation which expresses the time rate of change of the dependent variables (velocity components, etc.) at the grid points in terms of the source function, the dependent variables at the grid point, and the dependent variables at the centers of adjoining grid points (space derivatives). At the exterior of the lake these relations will be modified to include the external forces (sources) imposed by wind, bottom friction, river flows, etc.

(iii) An algorithm is designed (computer program) which takes the present state of the lake as defined by the values of the dependent variables at each of the grid points and systematically works through the volume of the lake using the relations developed in stage (ii) to evaluate the time derivatives, and by extrapolation the values of the dependent variables at the next step in time. This process is designed to repeat itself through a number of cycles sufficient to carry the calculations forward the desired length of time. The values of the dependent variables at the desired grid points are then printed out.

At this stage, numerical modelling takes on the aspects of a craft where skill and cunning separate the work of the journeyman from that of the apprentice. The goals are accuracy and stability of the finite difference schemes, economy of computation, and versatility of operation. The latter is extremely important as many different parameterizations of the bottom stresses, different wind-stress fields, bottom topography, etc. will be introduced in the process of testing and exploitation of the model.

(iv) A preliminary verification is carried out often by comparing the numerical solution against an analytical solution obtained for a simple case. This stage establishes that the machinery is working as intended.

Simons' model divides the lake horizontally into fixed, square prisms (5 km on a side for Lake Ontario), and vertically into four layers. The interfaces between the layers may be treated as permeable fixed surfaces through which the fluid moves vertically or as impermeable movable surfaces (free surface or thermocline). Density is treated as a function of temperature via a quadratic relationship approximating the equation of state. Thermal stratification and its attendant consequences on the field of motion are thus represented. This model has been carried through the preliminary stages of verification (Simons 1972), which have established the accuracy of the numerical procedures. The basic assumption remaining is the separation of scales of motion between mean motion and subgrid scale turbulence as represented by the eddy-diffusion hypotheses.

Data from the International Field Year on Lake Ontario provide good opportunities for the intercomparison of models with observations. A few singular episodes marked by storms such as the one discussed on p. 700 have been selected for detailed analysis, because of the improved chances of resolving cause-and-effect relations. The passage of tropical storm Agnes during June 22 and 23, 1972, provided one such episode (Staff C.C.I.W. unpublished data). Simons (1973) has analyzed current meter data from a vertical array of instruments at station 2, a location some 12 km south of Toronto. Output from the numerical model has been selected and presented so as to correspond to data collected by hypothetical current meters at the same locations. Comparisons are then made between observed and computed current meter records, and constitute the main part of the analysis.

Computation of water levels and comparison with actual observations suggest that the drag coefficient for wind stress based on direct turbulent flux measurements is too low, and this conclusion is also borne out by a comparison of observed and computed current speeds. The model drag coefficient was doubled to 3×10^{-3}, which gave better results.

The observed damping of vertically averaged horizontal velocity can be related to the bottom stress as a means of determining the best value of the coefficient used to parameterize the bottom friction.

The third parameter studied in this analysis is the coefficient of vertical eddy viscosity K'_z (see next section). The vertical transfer of momentum is one of the most important processes to consider in the simulation of the internal components of lake flows, as it is a major component in the coupling between horizontal layers of fluid. To achieve a reasonable correspondence between observed and computed currents, a number of formulations of the eddy viscosity coefficient were tested, the best of which was found to be of the form

$$K'_z = K_o + k\int_{t-T} |\tau_s|\,dt \qquad (15)$$

K_o is a minimum eddy viscosity coefficient (40 cm^2/s), $|\tau_s|$ is the absolute value of the wind stress, k is a nondimensional coefficient, and T is a lag period. K_o, k, and T are expected to be functions of depth, time, the current shear, and the density profile. In the case studied, good results were obtained by modifying the time-lag effect, and instead setting

$$K_z = 40 + k^1 (z,t)|\tau_z|\text{cm}^2/\text{s} \qquad (16)$$

where $k^1 = 0$ at a depth z until the vertical shear was large enough to provoke dynamic instability (see next section) and thereafter $k^1 = 100$. This procedure was important during and immediately after the storm. When K_z' was set at 250 cm²/s and maintained constant, the short period components of the internal solution were rapidly damped out. Fig. 12 shows the quality of the agreement between observed and computed currents at station 2.

Here is an excellent example where a numerical model may lead beyond an intuitive understanding of how a turbulent process is parameterized, to provide some solid clues for further development. The formulation of equations (15) and (16) are based on analysis of the current meter data; the lake appears to respond in such a fashion. This should provide a spur to fresh studies of the actual vertical exchange processes (see next section).

The modelling process has been examined in some detail in the hopes of convincing the reader that its products are not only simulations of an otherwise inaccessible lake circulation, but can also be powerful tools in understanding basic physical processes. Referring to the example of vertical diffusion of momentum, numerical modelling is an adjunct to both field experiments and theoretical formulations of lake processes, and the three techniques must necessarily progress together.

Biologists and chemists will be quick to recognize the practical benefits of physical modelling to their studies. They will be interested primarily in the degree to which lake circulations can successfully be reproduced by a model. Although there are without doubt theoretical and practical limitations as to how far computer simulations can progress, the results to date are encouraging. Attempts are being made at the Canada Centre for Inland Waters to use a numerical circulation model as one component of a seasonal nutrient budget model for a Great Lakes basin. It is anticipated that this approach will also pay off in a deeper understanding of lakes as integrated systems.

Vertical Transfers of Energy and Materials

In this section we shall discuss the dynamics of vertical exchange processes, with particular emphasis on vertically stratified conditions. We shall not discuss the distribution of light energy beneath the water surface, despite its obvious importance to lake biology.

The fundamental problem examined herein is how to describe quantitatively vertical motions, both turbulent and organized, as they affect the vertical distributions of nutrients, dissolved gases, and plankton.

As before, we can start with the conceptual framework provided by the classical theory of advection and diffusion in continuous media. As our length scale is now the depth of the water column, we choose to neglect variations in the horizontal occurring over this scale, a good approximation under most situations. Thus we have

$$\overset{(1)}{\frac{\partial s}{\partial t}} = -\overset{(2)}{\frac{\partial}{\partial z}(ws)} + \overset{(3)}{\frac{\partial}{\partial z}\left(K_z \frac{\partial s}{\partial z}\right)} + F \qquad (17)$$

where the symbols are those of equation (7).

If we are considering the distribution of a suspended material, we would have to add to (17) a term representing the transport of material by sinking or rising. This term would be of the form $-\frac{\partial}{\partial z}(w_s S)$ added to the right-hand side of (17), where w_s is the sinking velocity of the suspended particles (Riley et al. 1948; Burns and Pashley 1974).

The mean vertical velocity w, averaged over an hour or so, is usually small, less than 0.1 cm²/s, and beyond the capabilities of simple direct measurement. Significant mean vertical velocities occur sporadically near the shore and are associated with upwelling and downwelling. In this section, we are concerned with processes occurring beyond the influence of the lateral boundaries and for which w is effectively zero.

VERTICAL DIFFUSIVITIES BASED ON MEASURED FLUXES OF HEAT AND MOMENTUM

Up to this point we have referred to eddy-diffusion coefficients in a rather loose way — simply as being coefficients of proportionality between diffusive fluxes and concentration gradients. Now some distinctions must be drawn. In the case of the eddy diffusion of momentum, the transports are written

Vertical flux of the x component of momentum per unit mass =

$$\frac{\text{stress in } x \text{ direction across a plane perpendicular to the } z \text{ axis}}{\text{density}} = \frac{\tau_{zx}}{\rho}$$

$$= -K^z \frac{\partial U}{\partial z} \qquad (18)$$

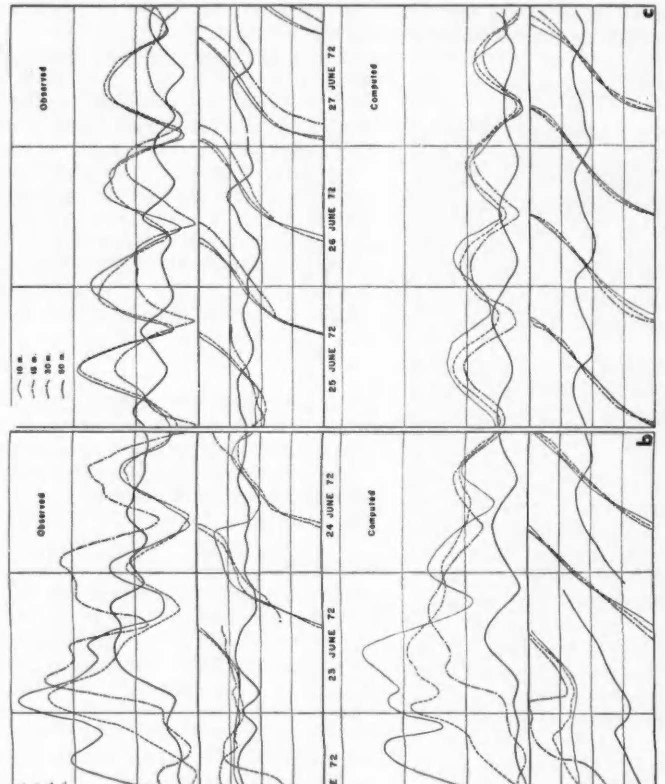


FIG. 12. Comparison between observed and computed currents at Station 2 for the "Agnes" episode, June 22–27, 1972 (Simons 1973) a). Three-day averages of currents. Simulation 1 uses a low value of vertical eddy viscosity. Simulation 2 uses a high value of vertical eddy viscosity. Simulation 3 again uses a high value of vertical eddy viscosity but presents computed currents from an adjacent grid point located 5 km to the north of Station 2; b) observed and computed currents at Station 2 during the "Agnes" storm using a vertical eddy viscosity in the form given by equation 16; c) observed and computed currents at Station 2 after the "Agnes" storm using the same (Fig. 12b) vertical eddy viscosity.

The symbol K_z' is the eddy-diffusion coefficient of momentum in the z direction, or the kinematic eddy viscosity in the z direction. Eddy-diffusion coefficients with primes will henceforth refer to the diffusion of momentum, and unprimed coefficients will refer to the diffusion of dissolved substances. The latter will be called eddy diffusivities. This distinction is necessary because under some conditions the eddy viscosity can differ from the eddy diffusivity. Usually the eddy viscosity is larger because momentum can be transferred by both pressure fluctuations and translation of water particles, whereas the diffusion of materials is accomplished only by the latter. As the eddy coefficients are at best approximate quantities, the assumption is often made that the eddy viscosity and the eddy diffusivity are equal. This is a useful working hypothesis, except under stably stratified conditions. Both coefficients, of course, have the dimensions of a kinematic viscosity, cm^2/s in cgs units.

In the case of vertical transport of heat, time series of temperature profiles, suitably time-averaged so as to remove short-term fluctuations and space-averaged to be representative of the whole lake basin, may be used to evaluate the time rate of change of temperature and the average vertical temperature gradient at various depths. A version of (17) is used to relate time and space derivatives

$$P(z)\,\frac{\partial \bar{T}}{\partial t} = \frac{\partial}{\partial z}\left(K_z\,P(z)\,\frac{\partial \bar{T}}{\partial z}\right) \qquad (19)$$

where $P(z)$ is the horizontal cross-sectional area of the lake at level z, and $\bar{T}(z,t)$ is the averaged temperature profile.

This formulation makes sense only when the horizontal transport of heat in and out of the basin (river flows) is negligible.

Equation 19 can be used in finite difference form to yield estimates of K_z at various depths and at various times; $\bar{T}\,(z,t)$ is typically determined from synoptic temperature surveys made from a ship (F. M. Boyce unpublished data). Sweers (1969) and Blanton (1973) have used similar methods to evaluate diffusion in lake thermoclines.

The method breaks down when vertical exchange by convection is underway (spring and fall overturning). The values of K_z obtained are representative of average conditions only, and "instantaneous" values would vary widely about the mean. Values of K_z determined by this method will be useful to chemists and biologists only in the same long-term average sense of the original data.

Measurements of horizontal currents as functions of time and depth also yield information on effective vertical turbulent transports. The framework for this discussion consists of the equations for mean horizontal motion far from the lateral boundaries of the lake, where the driving force is the surface wind stress.

The balance of forces and accelerations is written[8] formally.

$$\rho\left(\frac{\partial U}{\partial t} - fV\right) = -\frac{\partial}{\partial z}\,\tau_{zx}$$
$$\rho\left(\frac{\partial V}{\partial t} + fU\right) = -\frac{\partial}{\partial z}\,\tau_{zy} \qquad (20)$$

This model assumes the water to move as horizontal slabs; the acceleration of a slab is balanced by the Coriolis force and the net stress exerted on the slab by those above and below. τ_{zy} and τ_{zx} are the north and east components of the turbulent shear stress acting in a horizontal plane.

In absence of detailed measurements as to the actual distribution of τ_{zx} and τ_{zy} with depth, the customary practice has been to make various mathematically tractable hypotheses and then to test the computations against field measurements.

Ekman (1905) first proposed and solved equations (20) to explain the structure of wind driven currents in the upper active layer. He supposed that the stress was given by the eddy viscosity formulation (equation 18) and further assumed that the eddy viscosity was constant and that the horizontal velocity was zero on the bottom or tended to zero at great depths.

Although Ekman's solution is valuable because it suggests how the effect of the earth's rotation modifies the water column's response to a surface stress, it does not generally give satisfactory results. First, the supposition of a constant K_z' with depth does not fit well with the theory and observation of turbulence generated at a plane surface in a homogeneous fluid. Secondly, the presence of stable density gradients near the surface, which impose a gravitational restoring force countering any vertical displacements of fluid particles, is known to attenuate vertical turbulence and hence to reduce effective eddy viscosities. Versions of Ekman's theory which allow K_z' to vary with depth are potentially more realistic but mathematically much less tractable.

---

[8] These equations are an excellent example of the aperture vision provided by the Navier–Stokes equations.

A version of Ekman's model has been used by Gonella (1971) to explain wind-driven currents in the surface layer of the Mediterranean. He supposed that the shear stress would be given by (18) in the upper-mixed layer, but would vanish at the thermocline. This last assumption is commensurate with the tendency for a stable thermocline to inhibit vertical turbulence. Csanady (1972b) has applied Gonella's model to data obtained off Baie du Doré on Lake Huron and has deduced effective eddy viscosities, wind stresses, and response times for the upper-mixed layer. Csanady's response time is a measure of the time taken for the damping of transient component of the theoretical response of the mixed layer to changing winds, but it can also be considered as a time scale for vertical mixing of the epilimnion. For a 15 m thick epilimnion, typical values of eddy viscosities and response times are 100 cm^2/s and 1 h, respectively, under light (5 m/s at 4 m height) summer winds.

Pollard and Millard (1970) have achieved considerable success in predicting wind-driven currents in the upper-mixed layer using a version of (20) in which it is assumed that the horizontal stress vanishes at the lower boundary of the mixed layer and that the stress decreases linearly with depth below the surface. Physically, in the mean, the entire mixed layer moves horizontally as a slab. Gonella's model would converge on Pollard's and Millard's result if a large enough K_z' were assumed. Whatever the details of the process may be, the time scale of complete vertical mixing in a Great Lakes summer epilimnion under moderate winds is only a few hours.

Simons (1973) has studied data from vertical current meter strings located in Lake Ontario during June 1972 (IFYGL), an interval of time that bracketed tropical storm Agnes. Assuming that the shearing stress between adjacent layers is determined by (18) and that this stress is the principal agent by which momentum is transported downwards, he has evaluated effective eddy-diffusion coefficients as functions of both time and depth (Fig. 13).

During most of the period, the eddy viscosity at the 10-m level averages 50 cm^2/s, a value reported earlier by Platzman (1963). However, during the high winds associated with the passage of tropical storm Agnes, the effective eddy viscosity increased by a factor of 7.

This increase in vertical eddy viscosity can be related to the dynamic stability of the water column, which is to say the effectiveness of static stability of the water column due to stratification in the presence of strong vertical current shear (see page 718).

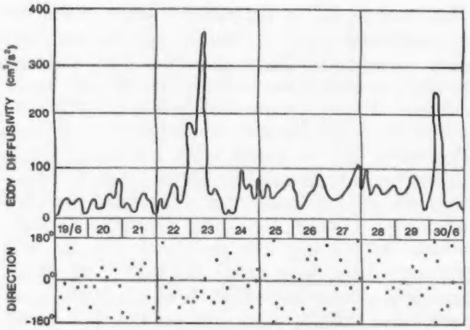


FIG. 13. Effective coefficient of vertical eddy viscosity at 10 m depth as computed from observed currents at Station 2 and 3-h averages of direction between wind stress and vertical shear (Simons 1973).

The formulation of Simons (1973) based on equation (18) depends critically on accurate determination of horizontal currents, as errors of measurement tend to be amplified by the differential nature of formula (18). In an alternate approach to this problem, Hamblin (1973 personal communication) has determined the averaged lag times between fluctuations in the wind stress and currents by a statistical method, and has related lag times to vertical eddy viscosities via an application of the time-dependent Ekman dynamics including horizontal pressure gradients. On the average, vertical viscosities of 5–10 cm^2/s were found at 30- and 50-m depths.

These spectacular variations should drive home the point that eddy viscosities and diffusivites are functions of the environmental conditions and not intrinsic properties of the fluid.

VERTICAL EXCHANGES BY ORGANIZED FLOW STRUCTURES: LANGMUIR VORTICES AND CONVECTION PHENOMENA

No discussion of vertical exchange processes in the epilimnion would be complete without mention of the Langmuir vortex phenomenon (Langmuir 1938). The observational facts seem consistent over a wide range of situations and have been reported by many observers. An excellent review of the physics of the phenomenon has been contributed by Faller (1971).

When the wind speed is in excess of a critical value (several meters/second), a banded structure appears on the water surface, with the bands or stripes lying in the direction of the wind. The stripes may be composed of bubbles, slicks of oily material, or accummulations of surface debris, all of which are indicative of the convergence of the surface waters. Surface water in the stripe seems to move downwind faster than water in between the stripes. Measurements of vertical velocities beneath the surface indicate downwellings beneath the stripes and upwellings between them. A picture emerges of a system composed of pairs of counter-rotating vortices, axes parallel to the wind direction, and of cross-sectional diameter comparable to the depth of the first stable layer. The vortices tend to occur more readily during conditions of neutral or decreasing stability at the surface, although they are also observed during conditions of increasing stability. The stripes tend to have an ephemeral existence; new stripes form between established stripes, established stripes fade from view. When the mixed layer is sufficiently deep, a hierarchy of stripes may be observed with weaker, more transient stripes appearing between the stronger persistent stripes related to the main thermocline depth. Observations by Harris and Lott (1973) in Lake Ontario are in accord with the above, and Harris (1974) in his studies of primary productivity (in conjunction with his investigation of the Langmuir circulations) makes the interesting observation that the vertical distribution of chlorophylls in the water column becomes uniform down to at least 5 m depth when the wind speed exceeds 4 m/s.

Several mechanisms have been proposed for the Langmuir circulations on the tacit assumption that the circulations are "ordered" flow structures for which a deterministic theory must eventually be found. Scott et al. (1969) and Faller (1971) discuss six mechanisms which may explain Langmuir circulation: (1) shearing instability of the Ekman Layer, (2) coupling of atmospheric vortices to the water, (3) thermal convection processes, (4) cross wind-stress variations caused by surface film, (5) transfer of energy of surface ripples to Langmuir cells by action of surface films, (6) interaction of surface wave trains. Some researchers (Csanady 1972b) maintain that Langmuir circulations are essentially a turbulent phenomenon and are the more visible because their physical dimensions lie at the outer limit of the spatial spectrum of turbulence.

Assaf et al. (1971) have conducted experiments in the ocean and in Lake Ontario, and have assembled convincing evidence for a hierarchy of vertical mixing mechanisms. Their findings, based on aircraft observations of dye plumes and drift cards, may be summarized: In light winds (5 knots) convergence lines with 3–6-m spacing are found almost everywhere. Under moderate winds, (10–30 knots) a second set of stripes appears coexistent with the first. The horizontal spacing of the second set of stripes is equal to the depth of the upper mixed layer. An Ekman spiral (velocity profile obtained by solving equations (20) under the eddy viscosity hypotheses of momentum transfer) may occur below the depth of the mixing layer. Finally, under strong winds (>30 knots) Langmuir-type circulations may extend to depths of 280 m, and the Ekman spiral regime is destroyed.

During summer and fall stratified conditions in the Great Lakes, the thermocline, which is exceptionally stable by oceanic conditions, determines the vertical dimensions of the largest Langmuir circulations. In winter, Assaf et al. (1971) report that the deep offshore regions of Lake Ontario exhibit vertical mixing phenomena similar to the oceans, with apparent Langmuir circulations extending to 100 m or more in depth.

The Langmuir vortex mechanism is consistent with the observed efficient transfer of momentum through the mixed layer under moderate winds. Assaf et al. (1971) propose a crude empirical model which yields a formula giving an estimate of eddy viscosity. This could be used to calculate vertical transports of a material in the epilimnion in the presence of the Langmuir circulations

$$K_s' \sim 0.18\, D\left(\frac{\tau_s}{\rho}\right)^{1/2} \tag{21}$$

where D is the depth of the mixing layer, τ_s is the wind stress, and ρ is the density of water. Substituting $\tau_s = \rho_a C_{Da} U_a^2$, we get

$$K_s' \sim 4.3 \times 10^{-4}\, U_a D \tag{22}$$

where U_a is the wind speed at 10 m height and $C_{Da} \cong 3 \times 10^{-3}$. Setting $D = 15$ m and $U_a = 5$ m/s, for example, K_s' becomes 270 cm^2/s, a value consistent with other estimates and large enough to ensure a rapid diffusion of momentum through the mixed layer (time scale $\sim$ 1 h).

Harris (1973), in his study of the effects of vertical mixing primary production, has been concerned with photoinhibition "hysteresis" effects due to the vertical cycling of phytoplankton cells through the water column. He finds that in July, vertical mixing under winds in excess of 3.5 m/s (Lake Ontario) was sufficient to ensure that plankton were exposed to high light intensities for brief periods only. Consequently, the photoinhibition effect observed when production measurements are made with moored 14 C bottles does not apply to natural production. However, deep Langmuir circulations in winter may have more complex effects on productivity; these cannot be determined until the details of the vertical circulations are known.

During periods of overturn, and particularly in the spring when atmospheric stability over the lakes is strong, vertical convection tends to become organized into cellular structures. Clusters of drogues (P. F. Hamblin unpublished data) have been observed to coalesce after a period of seemingly normal dispersion, which may indicate the presence of zones of surface convergence and downwelling. Assaf et al. (1971) report similar behavior in the oceans under conditions of light winds and surface cooling. Detailed surface thermal structure, obtained via airborne infrared scanners in the spring of the year, has revealed short-lived cellular patterns about 100 m across during clear calm conditions when the subsurface water column has a temperature of less than 4 C (Elder and Lane 1970). These structures are quickly destroyed by wind mixing.

Growth and Decay of the Thermocline

From a qualitative point of view, the basic mechanisms of thermocline formation and decay are fairly well established. Until recently, however (C. H. Mortimer unpublished data), our quantitative grasp of these processes has been limited to calculations based on observed thermal structure as opposed to predictions of structure from a knowledge of the input parameters and a workable theory.

There are two approaches which have been used with some success. The first is an extension of the vertical turbulent diffusion equation

$$\frac{\partial T}{\partial t} = \frac{\partial}{\partial z}\left(K_z\,(U_a,\ T(z),\ Z)\,\frac{\partial T}{\partial z}\right) \qquad (23)$$

where K_z is expressed as a function of wind velocity (stress), the temperature profile itself, and the depth. The upper boundary condition is

$$\left(K_z\,\frac{\partial T}{\partial z}\right)_s = \frac{-q_s}{\rho C_p} \qquad (24)$$

where q_s is the net heat flux at the surface and C_p is the specific heat. By experimenting with the functional dependence of K_z on wind stress and stability (temperature profile), a reasonably good correspondence can be obtained between observed and predicted temperature profiles (Sundaram and Rehm 1971) in particular cases.

The second approach consists of a mechanical energy budget for the water column, under the assumption that the transfer processes act uniformly over the water surface. A vertically integrated energy equation (25) for the water column may be written in words.

(1) Time rate of change of total kinetic energy + (2) Time rate of change of potential energy due to stratification

+ (3) Rate of energy loss by dissipation = (4) Direct production of turbulent energy at the surface (25)

+ (5) power input from the interaction of wind stress with surface currents + (6) rate of potential energy input due to heating and cooling of the water column.

On the left-hand side are found the three possible fates of energy introduced to the water column. On the right-hand side are found the major sources of energy acting across the water surface. Term (4), the direct production of turbulent energy at the water surface, has not been directly measured but is considered to include the contribution by breaking surface waves. Term (6) represents the conversion of thermal energy into mechanical energy by the expansion and contraction of the water column.

Without additional information, equation 25 is a self-evident tautology, as there is no a priori way of determining the partitioning of a given energy input among the three possible fates. To begin resolving this impasse, we first note that the potential energy of the water column is related to the mean thermal stratification and varies significantly over a seasonal time scale. It is increased by vertical mixing which varies the center of gravity of the column. However, the kinetic energy of the water column is introduced at shorter time scales related to the passage of storms. Moreover, we know that the response of the epilimnion to wind forcing, insofar as the transfer of momentum is concerned, is only a matter of hours. It would seem that term (1) of equation (25) is important in the epilimnion for short periods (hours) only and that, averaged over a few days, the two significant terms on the left-hand side of equation (25) are terms 2 and 3, the time rate of change of potential energy and the dissipation term. The next step depends on an experimental result obtained by Kato and Phillips (1969). They created in the laboratory a stably stratified fluid with a constant density gradient, and subjected this fluid to a constant surface stress via a moving grid. A uniformly mixed layer was formed at the surface of the fluid and the thickness of this layer increased as the experiment progressed. Except for the mechanism of stress generation, this situation is similar to the wind mixing of a stratified lake or ocean in the absence of heating or cooling, and is usually described as a turbulent entrainment process.[9] Over the range of conditions made possible by their apparatus, Kato and Phillips (1969) found that the rate of increase of potential energy of the water column was proportional to the power input from the surface stress. This is a remarkable result, because it implies that mechanical energy introduced at the surface is partitioned in a constant fashion between kinetic energy and dissipation on one hand, and vertical mixing (change in potential energy) on the other.

Edwards and Darbyshire (1973) arrived at a similar conclusion on the basis of a statistical analysis of temperature data from Lake Bala. They postulated that the rate at which the wind delivered energy to the water surface was given by

$$W = \tau_s \, k \, U_a^3 \quad (\text{ergs/cm}^2/\text{s}) \tag{26}$$

where τ_s is the wind stress at the surface and U_a is the wind speed at a given height above the surface (usually 10 m); k is a constant (0.0145) (Palmen 1931). Using the velocity squared law for the wind stress on the water, we get

$$W = K\rho_a \, C\rho_a \, U_a^3 \tag{27}$$

Edwards and Darbyshire's energy equation is

$$\underset{\text{time rate of change of potential energy}}{\frac{\partial P}{\partial t}} = MW \quad (\text{constant heat content}) \tag{28}$$

where M is a partitioning coefficient or "vertical wind-mixing efficiency." M was found to lie in the range 0–7%. Edwards and Darbyshire (1973) suggest that M depends on environmental conditions and is smaller for a deep thermocline. This is plausible and indeed necessary, because dissipation must ultimately control the depth to which significant amounts of turbulent energy can penetrate. (See also Turner 1973 p. 292). Note too that Edwards and Darbyshire's "wind-mixing efficiency" approach lumps together the terms (4) and (5) in equation (25) into an equivalent wind-stress effect (see Phillips 1966, p. 230).

We may thus write an equation relating the time rate of change of the potential energy P to the sum of the inputs of mechanical energy from the wind and heat transfer across the water surface. We first define P, the potential energy due to the stratification

$$P = g \int_{-H}^{o} z(\rho_o - \rho(z,t))dz \tag{29}$$

where H is the depth of the water, ρ_o is a reference density (average density of the column at the onset of stratification), and (z,t) is the distribution of density with depth and time. Following our usual convention, z is measured from the water surface with the positive direction being upwards. The energy equation may now be written

$$\frac{\partial P}{\partial t} = \overset{(1)}{\gamma_w \, U_a^3} + \overset{(2)}{\gamma_h \left(g \, \frac{\alpha_{vs}}{C_p}\right) q_s \, \delta} \tag{30}$$

where γ_w is an empirical coefficient incorporating the wind-drag coefficient, the coefficient k in equation (26), and the wind-mixing efficiency, M; α_{vs} is the volume coefficient of thermal expansion of water at the surface and C_p is the specific heat, q_s is the net heat flux across the water surface and δ is the vertical distance over which this heat flux is distributed. The parameter γ_h is a partitioning coefficient for the heat flux term, and represents the fraction of this energy used to mix the water column. γ_w, γ_h, and δ are all functions of environmental conditions. The evaluation of γ_h and δ is exceedingly difficult, because under net heating conditions the combination of evaporative cooling at the surface and absorption of solar radiation at depth can produce convective overturning and turbulence at the surface (Turner 1973). One can argue in a simpleminded way that $\gamma_h \sim 1$ under heating conditions (increase of stability at the surface), but under net cooling conditions and convective penetration to greater depths, no simple estimate can be given.

Kraus and Turner (1967) have tested various hypotheses concerning the relative importance of convectively generated turbulence on the cooling cycle of a water column and conclude that surface cooling eventually dominates the deepening of the thermocline, although the time at which significant deepening occurs in their model depends on wind input as well. For a deep mixed layer, such as is found in the Mediterranean, convection ensures a rapid distribution of the heat loss through the mixed layer but does not contribute to the deepening of the thermocline by entrainment (Anati 1971).

---

[9] The term "turbulent entrainment" is used to describe the interaction of a turbulent flow, jet, wake, etc. with a surrounding nonturbulent (or more weakly turbulent) fluid. Turbulent eddies adjacent to the calm fluid continually buffet the latter, and if the energy supply of the turbulent flow is sufficient, the neighboring regions of calm flow are incorporated into the turbulent region.

Equation (30) can be used to estimate the minimum wind speed necessary to provoke the turbulent entrainment of an interface at a depth D below the water surface under net heating conditions.

Before this process can start, the supply of turbulence to the surface must be enough to overcome the stability of any density gradient occurring between the surface ($z = 0$) and depth D, and to mix this layer to a state of virtual homogeneity. At this time the length δ is equal to D, as the mixing distributes the heat income uniformly to this depth. The condition for the onset of entrainment is then

$$\frac{\partial P}{\partial t} = 0 = \gamma_w U^3_{a_{crit}} + \gamma_h \, g \, \frac{\alpha_{vs}}{C_p} \, q_s D \qquad (31)$$

because any increase in windspeed beyond $U_{a_{crit}}$ will cause $\frac{\partial P}{\partial t}$ to be positive, indicating an active entrainment. Solving for $U_{a_{crit}}$, we get

$$U_{a_{crit}} = \left(\frac{\gamma_h \, \alpha_{vs}}{C_p \, \gamma w}\right)^{1/3} (-q_s D)^{1/3} \qquad (32)$$
$$= \beta \, (|q_s| D)^{1/3}$$

Using typical summertime values

$\gamma_h = 1$
$g = 980 \text{ cm/s}^2$
$\alpha vs = 10^{-4}/^\circ C$
$C_p = 1 \text{ cal/g/}^\circ C$
$w = 1.9 \times 10^{-9}$
$\beta = 372$ (cgs units)

For an epilimnion of 10 m thickness and a heating rate equivalent to 400 cal/cm^2 per day = 4.6×10^{-3} cal/cm^2 per s, $U_{a_{crit}}$ becomes 618 cm/s, or about 12 knots. This value is comparable to the values often quoted for the onset of Langmuir circulations in the epilimnion (Scott et al. 1969).

The energy approach to thermocline formation and decay is shored up by a quantity of daring hypotheses and "floating" constants equivalent to any other approach including the modified vertical diffusion equation (equation 23). It has the conceptual advantages, however, that it lies closer to the real physics of the problem, instead of sheltering behind the tattered skirts of the gradient diffusion hypothesis. The agreement between the predicted critical wind speed at which entrainment begins and the observed wind speeds at which Langmuir circulations begin, suggests that the energy approach may unify seemingly disparate phenomena. This possibility justifies, we believe, the more detailed attention given herein to this approach.

Equation (31) could also be considered as a "steady state" relation among mixed-layer depth, wind speed, and net surface heat flux under conditions of heating. The physical basis for the argument is the tendency for physical systems to exist in a state of minimum potential energy; equation (31) represents a dynamic balance between opposing forces which prevents a further increase of potential energy due to wind mixing. Rearranging (31) we get

$$D = \frac{\gamma_w \, U_a^3}{\gamma_h \, \frac{g^{\alpha} vs}{C_p} \, q_s} \qquad (33)$$

The application of such a model would be subject to the assumption that the time interval of adjustment of the mixed layer to a new set of inputs, U_a and q_s, is short compared with the time scales of fluctuation of the inputs. It might well apply to the formation of transient day-time thermoclines above the main thermocline, and if so, would be a means of estimating the partitioning coefficient, γ_w (Kitaigorodskii 1960).

Edwards and Darbyshire (1973) have constructed a predictive model of thermal structure using a form of the energy equation and obtain good correspondence between observed and computed temperature profiles in Lake Bala, for both heating and cooling conditions. Data collected during IFYGL on Lake Ontario will provide ample materials for a further testing and development of this model.

VERTICAL MIXING WITHIN THE THERMOCLINE — THE ROLE OF INTERNAL WAVES AND LARGE-SCALE VERTICAL SHEAR

In this paragraph we wish to discuss vertical mixing processes occurring beneath the upper mixed layer and in a region of stable stratificiaton. In this region there is no direct supply of energy from the surface-generated turbulence; kinetic energy for mixing must be drawn from the mean or organized horizontal motions. Both theory and experiment show that stably stratified fluids {for which $(\partial\rho/\partial_z) < 0$} become spontaneously unstable if the vertical gradient or shear of the horizontal velocities $|\frac{dU}{dz}|$ exceeds a critical value. This phenomenon is known as dynamic instability. A physical explanation can be suggested by imagining that a fluid particle is given a sudden initial vertical displacement from its rest position and released. In the absence of shear $(\frac{dU}{dz}) = 0)$ the particle is acted on by the restoring gravitational (buoyancy) forces which tend to return it to its original level. The potential energy of the initial displacement becomes the combined potential and kinetic energy of an internal wave. In the presence of vertical shears, vertical displacements of the particle subject it to horizontal forces due to the differences between the initial horizontal velocity and the horizontal velocity at the new level. If this velocity difference is large enough, this force tends to couple energy from the mean horizontal flow into the internal wave, causing it to grow in amplitude. If enough energy is available in the shearing motion, the initial disturbance is amplified and becomes turbulent; vertical mixing ensues until the velocity and density gradients are reduced. This behavior may be predicted from the value of a nondimensional parameter, called the gradient Richardson Number

$$R_i = \frac{-\frac{g}{\rho}\frac{\partial\rho}{\partial z}}{\left|\frac{dU}{dz}\right|^2} \tag{34}$$

$$\alpha\ \frac{\text{vertical gravitational restoring force}}{\text{vertical force tending to entrain particle}}$$

where ∂_ρ/∂_z and $\frac{dU}{dz}$ are the local vertical gradients of density and horizontal velocity. When $R_i = 0.25$ at a point in the fluid, internal waves spontaneously appear, grow, become unstable, and break, leading to a patch of turbulence and vertical mixing. The extent of the mixing depends on the energy available in the mean shear flow; as this energy is used up, the mixing reduces the local gradients of density and velocity, and the fluid becomes dynamically stable once more.

In lakes and oceans, the vertical shear of horizontal motion is caused by large-scale circulations and internal waves. Estimates of the overall Richardson's Number, R_{i_0}, based on measured velocity and density differences across the whole thermocline, are typically between 1 and 10 and are well away from the stability boundary, $R_i = 0.25$. Turner (1973) considers the potential and kinetic energy changes caused by the vertical mixing of a zone of uniform velocity and density gradients. The kinetic energy loss and the potential energy gain (due to mixing) exactly balance when $R_i = 1/2$. Such a balance would imply that all the energy for mixing could be supplied from the mean flow. The conclusion drawn by Turner is that smooth shear flows, where R_{i_0} assumes typical lake or oceanic values, do not contain enough available kinetic energy to mix vertically of their own accord.

Detailed examination of lake and oceanic vertical temperature profiles (Fig. 14) show that they rarely possess smooth gradients throughout, but are often more accurately described as systems of isothermal layers alternated with sheets of strong gradients. The vertical scale of the sheet and layer structure can be a matter of centimeters or can range to several meters. Vertical profiles of horizontal velocity at centimeter resolution are difficult to obtain, but limited evidence (see Kullenberg et al. 1973) exists to suggest that the sheets of strong density gradients are also zones of augmented velocity shear. Thus, microstructure seems to be the rule rather than the exception, and the questions are immediately raised — where does it come from and what is its role in vertical transfer processes?

Turner's (1973) conclusion on the energetics of smooth shear flow suggests that the formation of microstructure requires an additional energy input. The most likely source of this energy is internal waves. Orlanski and Bryan (1969) propose mechanisms whereby internal wave energy propagates vertically in a stratified fluid and is converted into turbulence by what can best be described as wave breaking. These mechanisms are distinct from shear instability. Woods (1968) convincingly demonstrates in both experiment and theory that a stable shear flow can be rendered locally unstable, in the Richardson Number sense, by the additional shear generated by a horizontally propagating internal wave. This process results in patches of turbulence, which vertically mix small regions. The collapse and spreading of these lenses of mixed water produces a more complex microstructure, and Woods and Wiley (1972) demonstrate that continuation of the process tends to develop a rich sheet and layer structure.

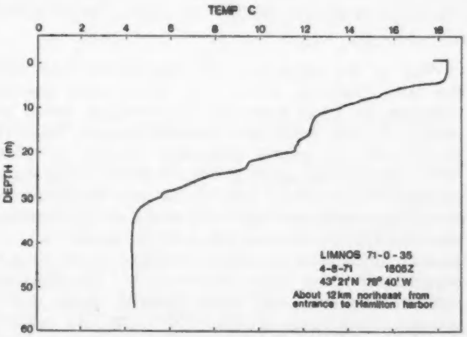


FIG. 14. An example of a summertime temperature profile taken in Lake Ontario showing evidence of thermal microstructure, at vertical scales ranging from 0.1 to 5 m.

An important point was made by Stewart (1969) that a zone of thickness H, across which there exists a velocity difference ΔU and a density difference $\Delta\rho$ such that

$$R_{io} = \frac{g\,\frac{\Delta\rho}{\rho}\,H}{(\Delta U)^2} > 0.25 \qquad (35)$$

indicating an overall dynamically stable layer, can be divided into sublayers of uniform gradients wherein the local Richardson's Number is everywhere less than 0.25, i.e. unstable and turbulent. Such a condition, however, could not be maintained (Turner 1973) without an external source of energy, such as that supplied by internal waves.

Measurements of short internal waves[10] in the Great Lakes are as yet rare. However, with the development of automated data-gathering equipment we can look forward to an increased research activity, leading to some sort of climatology from which we can eventually quantify the interaction between waves and turbulence. Observations made from moored platforms in calm weather often show bursts of periodic vertical motions in the thermocline which alternate with periods of relative calm (Mortimer et al. 1968; F. M. Boyce unpublished data). The periods of these motions are often about twice the local Brunt-Vaisala period, τ_B.

$$\tau_B = \frac{2\pi}{\left(\frac{-g}{\rho}\frac{\partial\rho}{\partial z}\right)^{1/2}} \qquad (36)$$

This period, which is determined by the density gradient, is the minimum period at which internal wave motions can exist (Groen 1948). Motions occurring at periods less than τ_B cannot be classified as internal waves and must be considered as turbulence. Records from towed thermistors made in calm weather also show a patchy occurrence of disturbances having wavelengths in the order of 50–100 m. These appear confined vertically to the zone of strongest density/temperature gradients, and are most frequently observed close to shore, particularly where the mean slope of the thermocline suggests the presence of large-scale flows (F. M. Boyce et al. unpublished data). At present we do not know where these waves come from and can only suggest a number of plausible mechanisms. One such mechanism which may be of importance has to do with the generation of internal surges and accompanying vertical mixing in the zone where the main thermocline intersects the bottom of the lake (Cacchione unpublished data). The energy for this mixing would be drawn from large-scale motions of the thermocline, particularly those associated with internal standing waves. The subsequent collapse of the mixed regions (Wu 1969; Schooley and Hughes 1972) can produce internal waves of about twice the local Brunt Vaisala period, which would then be observed propagating offshore. There is some fragmentary evidence to support this; namely, an apparent 17-h periodicity in the arrival of wave trains at an anchor station (F. M. Boyce unpublished data) and indications from repeated thermistor tows along a line perpendicular to the coast that some of the short-wave disturbances are propagating offshore (Boyce and Thompson 1973). To put these ideas on a firm basis we need to conduct experiments using arrays of three or more fixed-temperature profiles operating simultaneously (Zalkan 1970).

During periods of active wind forcing, we have observed short-wavelength internal waves all across the lake (F. M. Boyce et al. unpublished data). The waves in mid-lake were observed during the strong winds and disappeared as soon as the winds dropped. A local forcing is indicated, but again we can only guess as to what the mechanism may be. Prior to the August 9, 1972 storm, a period of calm winds and surface heating had occurred. Substantial temperature gradients extended to the surface, which expressed in terms of the Brunt-Vaisala period τ_B gave values in the range of 8–10 min at the surface over the central portion of the lake. During the storm, as we have mentioned, internal waves of about 200 m in length were observed in the main thermocline. The phase velocity of these waves, assuming them to be horizontally propagating, would be in the range 0.25–0.5 m/s, which would require their periods to be between 7 and 14 min. The overlapping of the range of short internal wave periods observed and the surface Brunt–Vaisala period observed prior to the storm, given the possibility of vertical propagation of internal wave energy in a continuously stratified fluid, strongly suggests that the thermocline waves are generated at the surface. This is a potentially important but as yet unexplored pathway of mechanical energy from the surface (Rhines 1973).

---

[10] Up to this point we have been rather loose with the term "internal wave." We have made specific reference to basin-wide internal standing waves or internal seiches which have periods ranging from 12 to 17 h. In the present discussion we refer to short, freely propagating internal waves having wavelengths ranging from several tens to several hundreds of meters, and periods measured in minutes. The motions associated with the internal seiches appear in our present discussion as slowly varying mean shears encompassing the whole thermocline. The field of motion associated with short internal waves is the internal counterpart of the wind-driven free surface wavefield, with the important difference that internal wave energy can propagate vertically as well as horizontally. This is an attribute of gravity waves in a continuously stratified medium as opposed to a discontinuously stratified fluid with free surfaces.

Experiments conducted by Kullenberg et al. (1973) are particularly revealing concerning the mechanisms of vertical mixing in the thermocline. They found that dye injected into a thermocline possessing the "sheet and layer" microstructure disperses in such a way that the highest concentrations of dye remain in the zones of strongest density gradients. Horizontal spreading is much slower than that observed in the epilimnion. Dye is removed from the layer of highest concentration by the active vertical turbulence in the isothermal layers above and below. It is not clear whether this diffusion is powered by injections of energy from short period internal waves, or whether longer period mean shears across the entire thermocline sustain the mid-thermocline turbulence. More detailed measurements of the vertical structure of currents will be needed to understand these phenomena.

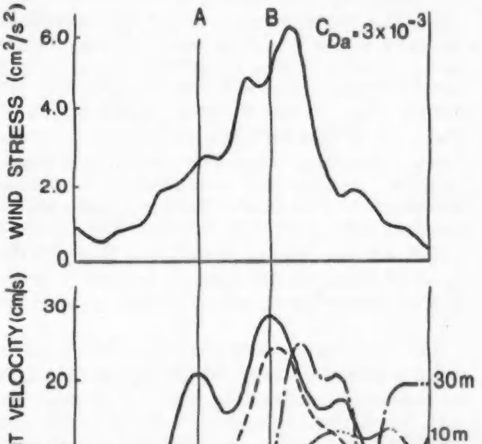


FIG. 15. Wind stress, current speeds, and temperatures observed at Station 2 during "Agnes" (Simons 1973). This time series illustrates the vertical diffusion of momentum from the surface downwards. At the instant of time marked A the stability at the first interface (10–15 m) is overcome and both momentum and heat are mixed down. The procedure is repeated for the second interface at time B. The transition to vertical mixing can be correlated to local Richardson numbers which approach the unstable limit.

Simons' (1973) analysis of current meter data mentioned earlier (see p. 693 and 711) indicates that in periods of weak stratification, large-scale dynamic instability is the mechanism accounting for the sudden increase in effective vertical eddy diffusion coefficients following the onset of strong winds. The current meter records at Station 2 all show a sudden increase in speed following the increase in wind stress, but at time lags which increase with depth (Fig. 15). At subsurface depths, the increase is sudden and occurs when the Richardson's Number (computed from the velocity difference observed between the level of interest and the one immediately above) decreases to near the theoretical stability limit.

In the foregoing discussion we have outlined some of the processes whereby the kinetic energy of mean horizontal motions is converted into turbulent energy supplying the vertical mixing processes. In basins the size of the Great Lakes, the energy associated with large-scale horizontal motions is unevenly distributed and is concentrated, as we shall presently discuss, in the coastal zones of the basins. To the extent that internal mixing processes are linked with the availability of kinetic energy of the mean motions, the existence of statistically different vertical mixing regimes must be one of the more interesting and significant aspects of Great Lakes limnology.

SUPPLY OF TURBULENCE TO THE HYPOLIMNION

In conditions of stable stratification, the supply of turbulent energy to the hypolimnion regions is primarily indirect. As Mortimer has pointed out (Mortimer 1952), currents associated with internal seiches and other baroclinic motions are stronger than those expected in the absence of stratification. The work done by these currents against bottom friction creates a turbulent boundary layer, and results in a greater vertical exchange of materials across the sediment–water interface than would be the case in still water. The shape of the summer temperature profile in the Central Basin of Lake

Erie suggests that the hypolimnion in that basin is at times even more turbulent than the epilimnion. Burns and Ross (1972) in their oxygen budget of the Central Basin hypolimnion, have observed that the turbulent entrainment process sometimes operates so as to entrain epilimnion water into the hypolimnion. The dynamic instability mechanisms can also be considered as potential suppliers of turbulence to the hypolimnion.

C. R. Murthy (unpublished data) has measured the diffusion of dye injected from a steady source beneath the thermocline in Lake Ontario. In terms of effective diffusivities he finds that horizontal diffusion is comparable to epilimnion processes, but vertical diffusion in the hypolimnion is much less active than that near the surface and is controlled by small-scale motions.

The Coastal Zone

The singularities of the coastal regions of large lakes will be apparent to all limnologists from the particular viewpoints of their own individual interests. Generally speaking, the coastal regions are areas of mutual interaction of all lake processes and are characterized by both extreme values and variability of most parameters. If one includes man's activities, in particular the disposal of waste heat from electrical power plants, then the physics of the shore zone is the result of a convergence of the four ancient elements, earth, air, water, and fire.

DYNAMIC STRUCTURE OF THE COASTAL ZONE

The simplified models discussed previously have provided some insight and provoked much discussion as to the structure of large-scale motions near the lateral boundaries of the lakes. Theoretical work initiated by Charney (1955) has been extended to large closed basins by Csanady (1967, 1968a, 1968b, 1971) and by Walin (1972). Bennett's (1973) simple, yet revealing model has been discussed. The general findings of these studies are that wave-like or periodic motions are strongest offshore and attenuated inshore, whereas the inverse is true for slowly varying currents. These conclusions are borne out by observations. In 1970 and 1972 (IFYGL), arrays of moored current meters were deployed by the Canada Centre for Inland Waters off Oshawa on the north shore of Lake Ontario. As the shoreline in the Oshawa area is of relatively simple configuration and free of any large-scale disturbing influence, such as major rivers, the flow patterns observed there ought to be representative in a general way of other Great Lakes shorelines.

From these data, the spectra of the kinetic energy of horizontal motions have been calculated (J. O. Blanton unpublished data). The composition of these spectra changes with distance from the shore (Fig. 16). The two spectra displayed here were obtained during the same time interval and from meters located 5 km apart. The spectra show that the energy contained in two frequency bands accounts for more than 70% of the total energy. The low frequency band contains the energy of motions having periods longer than 3 days. The high frequency band is centered on the inertial period (17.5 h) and contains the energy of motions having periods ranging from 12 to 20 h. Referring to the example presented in Fig. 16, the offshore station has 46% of the total kinetic energy in wave-like oscillations between 16–18-h period, whereas only 5% of the kinetic energy is found in this band at the inshore site. The time history of the current meters at the two sites shows that the motion observed 11 km offshore is clearly wave-like; the current meters rotate clockwise with a period of about 17 h. Inshore, the currents have a predominant alongshore component on which is superimposed meander-like oscillations of periods between 14 to 17 h. Similar findings in Lake Michigan have been reported by Birchfield and Davidson (1967). On the basis of limited data (Fig. 17) the point of transition off Oshawa between current-like and wave-like regimes is located about 8 km offshore.

The total kinetic energy per unit mass at a given depth is greater inshore, and this difference is most evident in the autumn (Fig. 18). This is consistent with the theoretical models discussed earlier and could not reasonably be attributed to regional differences in mean wind stress.

As most of the horizontal kinetic energy in the coastal zone (0–10 km offshore) is associated with motions which vary significantly over an interval of several days, the remainder of this discussion will be devoted to the thermal and current regimes associated with these long period motions.

During stratified conditions, Csanady (1972a) has correlated eastward flow along the northshore of Lake Ontario with an upwelled thermocline (depth of the thermocline increasing with distance offshore) and westward flow with a downwelled thermocline (depth of thermocline decreasing with distance offshore). The mean slope of the thermocline across Lake Ontario is between 10^4 and 10^5 (Sweers 1969), but the magnitude of the slope in the upwelling and downwelling zones often attains 10^{-3}. Moreover, these zones are confined within the coastal zone marked by the transition point in Fig. 17 (J. O. Blanton unpublished data). On the south shore, an upwelling regime is associated with westerly currents and a downwelling regime with easterly

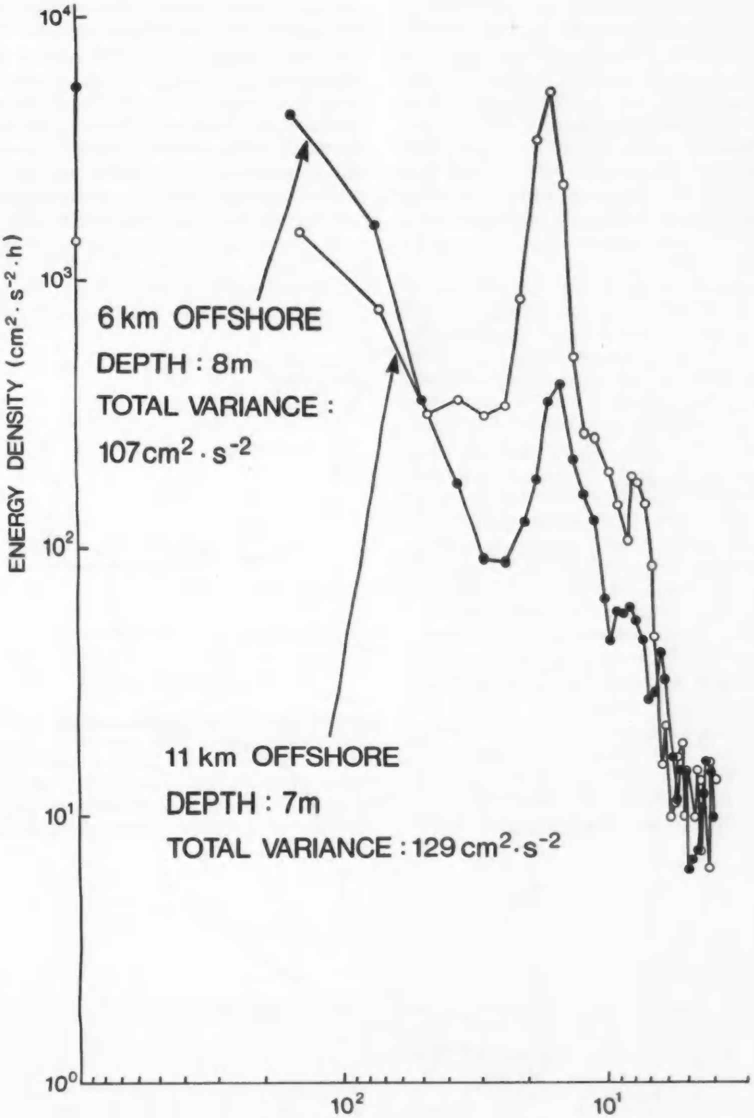


FIG. 16. Spectra of kinetic energy density for two locations only 5 km apart. There is a clear gap in the two spectra between motions having periods greater than 3 days and for motions having periods near the theoretical inertial period. The currents 11 km offshore have much higher energy in the latter when compared to those only 6 km offshore.

currents (Scott 1973). This behavior is consistent with simple circulation theories (Bennett 1973.)

The changeovers from upwelling to downwelling regimes and vice-versa are of particular interest to nearshore biology and chemistry studies. A typical downwelling–upwelling changeover (Fig. 18) is accompanied by marked changes in the thermal structure in the first 8 km offshore, over a period of 5 days. The benthic boundary in the coastal zone, formerly exposed to epilimnion water, is now exposed to hypolimnion water. Furthermore, such changeovers are accompanied by potentially large onshore–offshore transports of materials in both unstratified and stratified conditions.

As one might expect, the coastal zone regime responds most strongly to the component of wind along the main axis of the lake, and each major shift in this component is reflected in major adjustments in the coastal regime. A reversal of wind direction, if sufficiently prolonged, leads to a reversal of the coastal regime. In a changeover from downwelling to upwelling, for example, epilimnion water

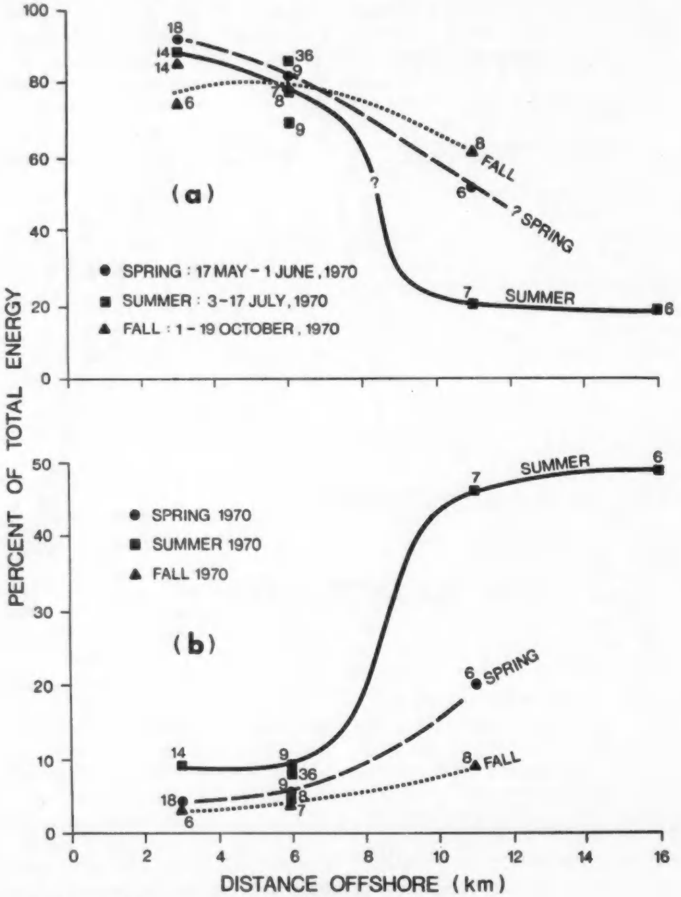


FIG. 17. Kinetic energy in motion having periods a) exceeding 3 days, and b) between 16 and 18 h. Energy is given as a percent of the total as defined in Fig. 18. Numbers adjacent to the data points are depths of observation in meters below the lake surface. The trend lines are an eye fit to shallowest observations (J. O. Blanton unpublished data: some characteristics of nearshore currents along the north shore of Lake Ontario.)

formerly against the shoreline must move offshore as the thermocline depth decreases, and if the upwelling is sufficiently strong, hypolimnion water may appear on the surface. Moreover, because the net wind stress force per unit mass of fluid in a vertically mixed layer is inversely proportional to the thickness of the layer, the shallow nearshore zones respond more quickly to a change in wind stress, and with an overall greater change in the current speed than the offshore areas. Changes in wind regime then produce transient but marked horizontal current shears. (Fig. 19). It is well known that dispersal of dissolved materials is more rapid in shear flows (Okubo 1968), consequently the onshore–offshore exchange resulting from upwelling and downwelling at the shore is accompanied by increased horizontal mixing.

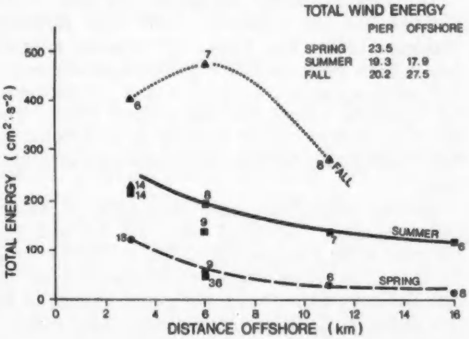


FIG. 18. Total kinetic energy (mean speed squared plus the variance) for some simultaneous current meter records off Oshawa in 1970. Total "energy" for wind records is given in m^2/s^2. Numbers adjacent to each data point are as stated for Fig. 17. The trend lines are an eye fit to shallowest observations. (Blanton 1973).

During periods of calm or of steady meteorological conditions, the coastal currents vary but little. Effluents from shoreline sources tend to hug the shore (Csanady 1970; Murthy 1972), with little cross-stream dispersion. Okubo (1970, 1973) has attributed this entrapment phenomenon to turbulent eddies shed by the irregular shoreline. This mechanism is akin to the mechanism of vertical turbulent entrainment, wherein the nonturbulent fluid is entrained into the turbulent fluid. This idea suggests that there may be two coastal zones: the outer zone, extending to the limit of upwelling and downwelling (8–10 km); and the inner zone, comprising a sort of turbulent boundary layer where the source of turbulence is the interaction of the mean flow with shoreline irregularities. Palmer (1973) has measured horizontal turbulence spectra using both current meters and hot-film anemometers at two sites, one near the shore (1 km distance) and another well offshore. The nearshore spectrum contains more energy at high frequencies and is similar to the type of spectrum found in turbulent boundary layers.

From a resource management point of view, the behavior of effluent plumes generated by shoreline sources is of great interest. There are three basic situations to consider. During periods of steady alongshore currents, the lakeward dispersion of the effluent is relatively feeble and the downstream shoreline is "fumigated." During periods of weak or zero alongshore currents, a pool of high concentrations of the effluent material will tend to accumulate near the discharge. During periods of current reversal, however, lakeward dispersion is rapid; estimates of eddy-diffusion coefficient obtained under changing currents are several times

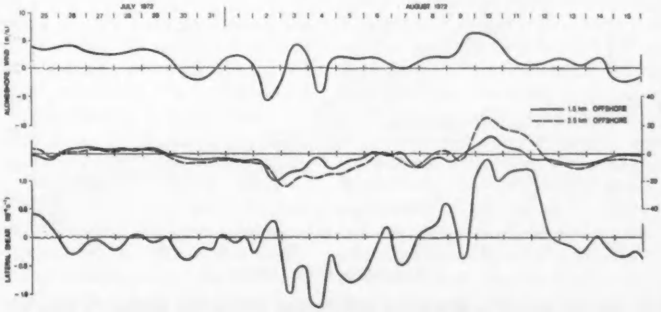


FIG. 19. The distribution in time of lateral shear in the alongshore component of nearshore currents near Oshawa, Lake Ontario. Eastward currents are positive and the shear is defined as velocity at 2.5 km minus velocity at 1.5 km divided by the distance separating the two observation points. Note the low shear values during the relatively steady wind on July 25 through 29, and compare with the high shears observed after a storm on August 9.

larger than eddy diffusivities measured during steady currents (Murthy 1972). The eddy coefficients measured under changing conditions are not useful for predictions of dispersion, but serve as a posteriori estimates of the relative efficiency of the dispersal process. It is ironic that the area of the lakes where diffusion predictions would be most useful is the area of most rapidly changing regimes, and hence the least amenable to deterministic predictions.

The Thermal Bar

As the spring sun begins warming the Great Lakes, the surface waters are below the temperature of maximum density (4 C). The water in shallow coastal areas warms more rapidly than the waters in deeper areas, so that by May in the southern Great Lakes the nearshore waters are above 4 C, whereas those in the middle lake are still below 4 C. Thus, there is a zone in between where the water density is greater than the surrounding water both nearshore and offshore, and sinking occurs. A thermal profile across the north shore of Lake Ontario (Fig. 20) illustrates the stratified nature of the waters nearshore. This zone has been called the "thermal bar" (Rodgers 1965; Tikhomirov 1963).

Rodgers (1965, his figure 7) first proposed a conceptual model of the circulation associated with the thermal bar in the Great Lakes, where sinking was shown to occur near the 4 C zone with surface convergence into this zone from the warm and from the cold side of the bar. The surface waters in the coastal zone and in the mid-lake region were replaced by a slow upwelling of deeper water. As heating of the nearshore waters proceeds, the bar advances offshore, leaving behind a weakly stratified nearshore water mass (Fig. 19). Thus, the thermal bar appears to mark the onset of summer stratification. The sinking water associated with the surface convergence in the vicinity of the bar is thought to form the water mass associated with the hypolimnion of the lake once the entire lake becomes stratified (Rodgers 1966). A pathway of mechanical and potential energy is thus established which links the coastal zone of the lake to the deep central portions.

The stratified waters on the coastal side of the thermal bar are correlated with high turbidity (Rodgers 1968). The source of turbidity appears due to both inorganic and organic suspended material, most probably from spring runoff and accelerated biological activity in the warmer water. The effects of the thermal bar on chemical and biological lake systems have not been determined in a definitive way.

Various researchers have attempted to model the circulation associated with the thermal bar (Bennett 1971; Csanady 1971; Elliott 1971; Huang 1972). In the latter stages of development of the bar, the nearshore waters are warm enough to be less dense than the offshore waters. This induces

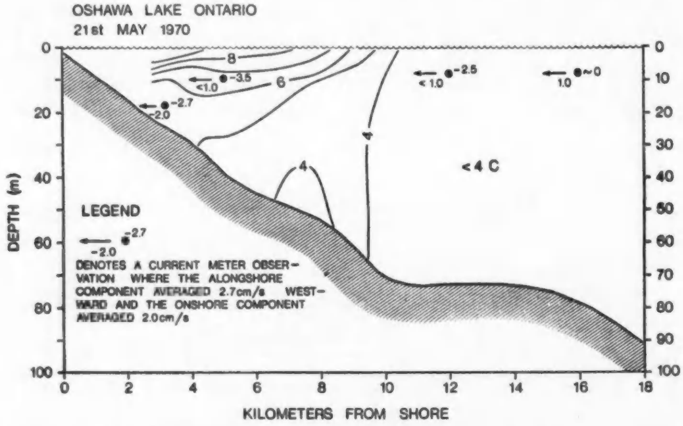


Fig. 20. A typical temperature distribution across the nearshore zone off Oshawa during the thermal bar period. Current meter data were obtained at locations denoted by ●. The alongshore and onshore components are averages of hourly values from May 15 to June 1, 1970. Flow averaged westward with a small onshore component in the nearshore zone. Flow at the offshore location had a negligible alongshore component with flow predominantly toward the thermal bar. Strongest currents were observed at the point closest to shore.

an offshore pressure gradient, and the resulting offshore motion is presumably deflected by the Coriolis force (counter clockwise shoreline circulation for large lakes in the northern hemisphere). The adjustment to alongshore flow occurs within a shorebound zone of 10–15 km width (Csanady 1971, 1972a). Current measurements along the north shore of Lake Ontario, averaged over 2 or 3 wk in spring, confirm the postulated direction of the currents (Fig. 19).

The spring thermoclines in the northern coastal zone of Lake Ontario can assume "wedge" or "lens" shapes. The former appear associated with westward currents, the latter with eastward currents. Csanady (1972a) points out that these shapes may be explained in terms of wind-driven alongshore currents modified by the earth's rotation.

Conclusions

Throughout the preceding Chapters there has been woven, implicitly or otherwise, the idea that research into the various physical processes must eventually come together into an upward spiralling hierarchy of supermodels. Fortuitous and ephemeral combinations of circumstance allow us to investigate some of the processes singly, but we know that they all act together, and our ultimate goal is knowledge of the sum of their actions. In this sense, numerical models along the lines of those developed by meteorologists and applied to lakes by Simons (1971, 1972, 1973) are the present culmination of our art, despite the wealth of detailed information we may possess on particular processes studied in isolation. Work with these models has demonstrated what we do not know and forces us into a continuing confrontation with the limitations of our present ideas.

The basic problem, as we have stated earlier, stems from the multiplicity of scales of motion in large lakes, and the consequent difficulties, both theoretical and computational, of representing them in terms of the large-scale average flow variables which we are able to compute over the entire lake. There is an element of "all-or-nothing" in this enterprise, arising from the closed nature of the lake basins and the resultant organization of horizontal motions occurring at time scales of more than a day to suit the confining boundaries.

It is ironic that the refinement of our tools of measurement, to the point where they begin to reveal some of the details of lake structure and motion, has not led to an increased confidence in our predictive abilities, but rather to an increased confusion in the face of a bewildering complexity of partially understood but potentially important phenomena. A good example of such a phenomenon is the role of short internal waves in vertical mixing. The catalog of lake motions available for study has grown fatter, whereas that containing the promises of lake systems modelling has become thinner. In the long run, this is a sobering but useful experience, and it is fitting that we compile our list of high priority areas of physical research in a state of humility.

It has long been known that estimates of wind stress based on direct measurement in the atmosphere above the water surface are too small to account for observed wind set-ups and large-scale currents. Models of lake motions have been brought into closer correspondence with observations by arbitrarily increasing the wind stress to between two and three times its observed value. This has usually been a satisfactory procedure for vertically integrated models, such as those used for the prediction of storm surges. The surface wave field is commonly held to be the source of the additional momentum (and energy). However, attempts to model the vertical structure of lake currents (T. J. Simons 1974 personal communication) having met with some success at long time scales (days) using an augmented wind stress, now suggests that this approach, coupled with the conventional eddy viscosity parameterization of the vertical transfer of momentum, may lead to shortcomings in the simulation of higher frequency motions. There is a double problem here, one in elucidating the contribution of surface waves (most likely through forward breaking) to the net mechanical energy transfer, and the other in determining the mechanisms of energy and momentum transfer below the water surface. It is important to remember that vertical eddy viscosities are computed from large scale flow variables and in fact reveal nothing about the mechanism of momentum transfer. Most, if not all, of the previous section leads to the conclusion that the time is ripe for detailed studies of the structure of turbulence in the upper active layers. This problem is common to the oceans as well as lakes, and the wish to explore directly the properties of the transfer mechanisms is expressed in a substantial portion of today's oceanographic literature. Specifically, we are going to need the underwater equivalent of micro-meteorological measurements, but at compressed vertical scales. To study the contributions made by surface waves we shall need to make some measurements of turbulent velocity fluctuations at distances fixed with respect to the moving water surface. Simultaneous measurements of current and velocity profiles at vertical resolutions of the order of a few centimeters will be invaluable.

The technical, analytical, and theoretical prerequisites to any real progress are large, and we can count on years of effort. Although a number of different experiments are indicated, much would be gained by conducting them concurrently with biological and chemical investigations. We hope that joint programs involving many researchers can be carried out in the near future.

An area of research of great practical importance is the study of lake coastal zones. In these studies we can no longer rely on assumptions that local vertically acting processes can be distinguished from processes driven by the interaction of lake–basin-scale motions with an irregular shoreline. The prospects of a deterministic modelling approach to the scales of motion affecting biological and chemical interactions in the coastal zone are less bright than for the larger-scale motions offshore. From a numerical modelling point of view alone, the increased horizontal and vertical resolution needed near the coast and the requirement to simulate the driving large-scale motions, together tax the finite memory capacity of the largest computers, let alone the task of assembling even more complex programs. In a sense, this situation is analogous to the problem of meteorological predictions wherein it is possible to forecast accurately the evolution of large-scale weather systems, at the same time being quite uncertain concerning the predictions of daily local surface conditions. For the immediate future, a statistical or climatological approach seems to be warranted. In a given area, the kinds of information useful to water resource management are seasonal temperature structure of the coastal zone average values, extremes, and standard deviations, the width of the coastal current zone and strength of the currents, the nature of the inner coastal boundary with reference to the phenomenon of coastal entrapment, and most important, the statistics of major current reversals and of periods of stagnation in the coastal zone. With this kind of information, worst-case engineering estimates can be made of the effluent concentrations to be expected from a proposed discharge.

We anticipate that climatological measurements could be generalized or extrapolated to yield a Great Lakes coastal climatology, in which the above characteristics would be expressed in terms of shoreline location, orientation to the prevailing winds and the main axis of the lake basin, bottom topography, and shoreline configuration. Specific measurements would include long-term current and temperature measurements within an array of locations both perpendicular and parallel to the coasts, three-dimensional internal wave arrays (time-dependent temperature structure at time scales of minutes) coupled with detailed vertical profiles of velocity, together with supporting ship-, launch-, and aircraft-based surveys. Again, such experiments should be planned on a broad interdisciplinary basis and include as wide a spectrum of experimentation as can be assembled.

Turning once more to the numerical models as the integrator of our collective knowledge, the feeling is strengthening that a different and more objective approach is needed to verify model performance against lake behavior. In the past, we have selected singular episodes of history bracketing major storms, on the assumption that the cause-and-effect relations ought to be the most clear during these intervals. This approach has served us well. However, a fairer test would consist of comparing model and lake responses over much longer time periods, so that a statistical rather than a subjective measure of the success of the model can be obtained. This new approach could be termed an operational modelling program, and would consist essentially of running the model using regularly available meteorological data on a daily basis. Concurrent field data in the form of long-term records of currents, lake water levels and temperatures would have to be collected at a few well-chosen locations, to provide a basis for the systematic and continuing evaluation of the model.

In a final paragraph it is difficult to resist the dramatic impulse to seek out a resounding and poetic conclusion. We hope that this essay will convince its readers there are few simple answers and that it will set in a fitting perspective the tendency for physicists to hide the pimply nakedness of doubtful hypotheses behind a cloak of mathematical elegance. Although the processes are acted out beneath the keels of our ships and as we swim on our backs in the summer sun, we are not unlike astronomers explaining the whorls of a distant galaxy.

Acknowledgments

The first person plural has been used throughout the work as a token of the collective nature of the undertaking in which I have served primarily as spokesman for the Physical Limnology Section of Lakes Research Division, Canada Centre for Inland Waters. I am indebted to T. J. Simons, C. R. Murthy, and P. F. Hamblin for valuable criticism and encouragement, and particularly to J. O. Blanton, who also organized the material for the chapter on the Coastal Zone.

ANATI, D. A. 1971. On the mechanism of the deep mixed layer formation during Medoc '69. Cah. Oceanogr. 23: 427–443.

ASSAF, G., R. GERARD, AND A. L. GORDON. 1971. Some mechanisms of oceanic mixing revealed in aerial photographs. J. Geophys. Res. 76: 6550–6572.

BATCHELOR, G. K. 1947. Kolmogoroff's theory of locally isotropic turbulence. Proc. Camb. Philos. Soc. 43: 533–559.

1950. The application of the similarity law of turbulence to atmospheric diffusion. Q. J. R. Meteorol. Soc. 76: 133.

1967. An introduction to fluid dynamics. Cambridge Univ. Press, Cambridge. 615 p.

Bennett, J. R. 1971. Thermally-driven lake currents during the spring and fall transition periods, p. 535–544. *In* Proc. 14th Conf. Great Lakes Res. Int. Assoc. Great Lakes Res.

1973. On the dynamics of wind driven lake currents. Univ. Wis. Mar. Stud. Cent. Contrib. 15.

Birchfield, G. E., and D. R. Davidson. 1967. A case study of coastal currents in Lake Michigan, p. 264–273. *In* Proc. 10th Conf. Great Lakes Res. Univ. Mich. Great Lakes Res. Div.

Blanton, J. O. 1973. Rates of vertical entrainment in stratified lakes, p. 301–305. *In* Proc. Int. Symp. Hydrology of Lakes. Helsinki, July 1973. Int. Assoc. Hydrol. Sci. Publ. 109.

Boyce, F. M., and K. P. B. Thomson. 1973. Internal wave trains of finite amplitude in Lake Ontario. Dep. Environ., Inland Waters Directorate Sci. Series. No. 27. 6. p.

Burns, N. M., and C. Ross. 1972. Project Hypo — an intensive study of the Lake Erie central basin hypolimnion and related surface water phenomena. Can. Cent. Inland Waters Pap. No. 6, and US Environ. Prot. Agency Tech. Rep. TS-05-71-28-24.

Burns, N. M., and A. E. Pashley. 1974. In situ measurement of the settling velocity profile of particulate organic carbon in Lake Ontario. J. Fish. Res. Board Can. 31: 291–297.

Charney, J. G. 1955. The generation of oceanic currents by wind. J. Mar. Res. 28: 477–498.

Csanady, G. T. 1967. Large scale motion in the Great Lakes. J. Geophys. Res. 72: 4151–4161.

1968a. Wind-driven summer circulation in the Great Lakes. J. Geophys. Res. 73: 2579–2589.

1968b. Motions in a model Great Lake due to a suddenly imposed wind. J. Geophys. Res. 73: 6435–6447.

1970. Coastal entrapment in Lake Huron. Adances in Water Pollution Reasearch, Sam Francisco and Hawaii, 1970. International Association on Water Pollution Reasearch 1: 1–7.

1971. On the equilibrium shape of the thermocline in a shore zone. J. Phys. Oceanogr. 1: 263–270.

1972a. Response of large stratified lakes to wind. J. Phys. Oceanogr. 2: 3–13.

1972b. Frictional currents in the mixed layer at the sea surface. J. Phys. Oceanogr. 2: 498–508.

1972c. The coastal boundary layer in Lake Ontario. Part I: The spring regime. J. Phys. Oceanogr. 2: 41–53.

1972d. The coastal boundary layer in Lake Ontario. Part II: The summer-fall regime. J. Phys. Oceanogr. 2: 168–176.

1973. Turbulent diffusion in the environment. D. Reidel Publ. Co., Dordrecht, Holland. 248 p.

Edwards, A., and J. Darbyshire. 1973. Models of a lacustrine thermocline. Extr. Mém. Soc. Roy. Sci. Liége, 6^e Ser. Tome 4: 81–101.

Ekman, V. W. 1905. On the influence of the earth's rotation on ocean currents. Ark. Mat. Astron. Fys., Roy. Swed. Acad. Sci. 2(11): 1–52.

Elder, F. C., and R. K. Lane. 1970. Some evidence of meteorologically related characteristics of lake surface temperature structure, p. 347–359. *In* Proc. 13th Conf. Great Lakes Res. Int. Assoc. Great Lakes Res.

Elliott, G. H. 1971. A mathematical study of the thermal bar, p. 545–554. *In* Proc. 14th Conf. Great Lakes Res. Int. Assoc. Great Lakes Res.

Faller, A. V. 1971. Oceanic turbulence and the Langmuir circulations. Annu. Rev. Ecol. Syst. 2: 201–236.

Gonella, J. 1971. The drift current from observations made on the Bouee Laboratoire. Cah. Oceanogr. 23: 19–33.

Groen, P. 1948. Contribution to the theory of internal waves. Kon. Ned. Meteorol. Inst. Meded. Verh. (Ser. B) II(11): 2–23.

Harris, G. P. 1974. Vertical mixing mechanisms and their effects on primary production. Dep. Environ., Inland Waters Branch Sci. Ser. Rep. (In press)

Harris, G. P., and J. N. A. Lott. 1973. Observations of Langmuir circulations in Lake Ontario. Limnol. Oceanogr. 18: 584–589.

Huang, J. C. K. 1972. The thermal bar. Geophys. Fluid Dyn. 3: 1–25.

Kato, H., and O. M. Phillips. 1969. On the penetration of a turbulent layer into stratified fluid. J. Fluid Mech. 37: 643–655.

Kitaigorodski, S. A. 1960. On the computation of the thickness of the wind-mixing layer in the ocean. Bull. Acad. Sci. USSR Geophys. Ser. 3: 284–287.

Kraus, E. B., and J. S. Turner. 1967. A one dimensional model of the seasonal thermocline. II, The general theory and its consequences. Tellus 19: 98–106.

Kullenberg, G., C. R. Murthy, and H. Westerberg. 1973. Experimental studies of the diffusion characteristics in the thermocline and hypolimnion regions of Lake Ontario, p. 774–790. *In* Proc. 16th Conf. Great Lakes Res., Sandusky, Ohio. Int. Assoc. Great Lakes Res.

Langmuir, I. 1938. Surface motion of water induced by wind. Science 87: 119–123.

Lorentz, E. N. 1963. The predictability of hydrodynamic flow. N.Y. Acad. Sci. Transl. Ser. II (25): 409–432.

Mortimer, C. H. 1952. Water movements in lakes during summer stratification; evidence from the distribution of temperature in Windermere. Philos. Trans. R. Soc. Lond. Ser. B. Biol. Sci. 236(635): 355–404.

1971. Large scale oscillatory motions and seasonal temperature changes in Lake Michigan and Lake Ontario. Univ. Wis.-Milw. Cent. Great Lakes Stud. Spec. Rep. No. 12.

Mortimer, C. H., D. C. McNaught, and K. M. Stewart. 1968. Short internal waves near their high-frequency limit in central Lake Michigan, p. 454–469. *In* Proc. 11th Conf. Great Lakes Res., Int. Assoc. Great Lakes Res.

Murthy, C. R. 1972. Complex diffusion processes in coastal currents of a lake. J. Phys. Oceanogr. 2: 80–90.

1973. Horizontal diffusion in lake currents, p. 327–334. *In* Proc. Int. Symp. Hydrology of Lakes, Helsinki, July 1973. Int. Assoc. Hydrol. Sci. Publ. 109.

Okubo, A. 1968. Some remarks on the importance of the "shear effect" on horizontalt diffusion. J. Oceanogr. Soc. Japan 24: 60–69.

1970. A mathematical model for the entrapment phenomenon. Trans. Am. Geophys. Union 51: 319.

1971. Oceanic diffusion diagrams. Deep-Sea Res. 18: 789–802.

1973. Effect of shoreline irregularities on stream wise dispersion in estuaries and other embayments. Neth. J. Sea Res. 2: 213–224.

Oort, A. H., and A. Taylor. 1969. On the kinetic energy spectrum near the ground. Mon. Weather Rev. 97: 623–636.

Orlanski, I., and K. Bryan. 1969. Formation of the thermocline step structure by large amplitude internal gravity waves. J. Geophys. Res. 74: 6975–6983.

Ozimodov, R. V. 1965. Energy distribution between oceanic motion of different scales. Bull. Acad. Sci. USSR Atmos. Oceanic Phys. 1: 257–261.

Palmen, E. 1931. Zur Bestimmung des Triftstromes aus Terminbeobachtungen. J. Cons. Int. Explor. Mer. 6: 3.

Palmer, M. D. 1973. Some kinetic energy spectra in a nearshore region of Lake Ontario. J. Geophys. Res. 78: 3585–3596.

Phillips, O. M. 1966. The dynamics of the upper ocean. Cambridge Univ. Press, Cambridge. 261 p.

Platzman, G. W. 1963. The dynamic prediction of wind tides on Lake Erie. Meteorol. Monogr. 4 (26): 44 p.

Pollard, R. T., and R. C. Millard Jr. 1970. Comparison between observed and simulated wind generated inertial oscillations. Deep-Sea Res. 17: 813–822.

Rao, D. B., and T. S. Murty. 1970. Calculation of the steady state wind driven circulations in Lake Ontario. Arch. Met. Geophys. Bioklim. (Ser. A) 19: 195–210.

Rhines, P. 1973. Observations of the energy-containing oceanic eddies, and theoretical models of waves and turbulence. Boundary-layer Meteorol. 4: 345–360.

Riley, G. A., H. Stommel, and D. F. Bumpus. 1949. Quantitative ecology of the plankton of the western North Atlantic. Bull. Bingham Oceanogr. Collect. Yale Univ. 12(3): 1–169.

Rodgers, G. K. 1965. The thermal bar in the Laurentian Great Lakes, p. 358–363. *In* Proc. 8th Conf. Great Lakes Res. Univ. Mich. Great Lakes Res. Div. Publ. 13.

1966. A note on thermocline development and the thermal bar in Lake Ontario, p. 401–405. *In* Symposium of Garda. Int. Assoc. Sci. Hydrol. Vol. 1.

1968. Heat advection within Lake Ontario in spring and surface water transparency associated with the thermal bar, p. 480–486. *In* Proc. 11th Conf. Great Lakes Res., Int. Assoc. Great Lakes Res.

Schooley, A. H., and B. A. Hughes. 1972. An experimental and theoretical study of internal waves generated by the collapse of a two-dimensional mixed region in a density gradient. J. Fluid Mech. 51: 159–175.

Scott, J. T. 1973. U.S. IFYGL Coastal Chain Program Rep. 1c: Basic data for the Olcott Coastal Chain. Natl. Oceanic Atmos. Admin. Atmos. Sci. Res. Cent. Rep. No. 227C.

Scott, J. T., G. E. Myer, R. Stewart, and E. G. Walther. 1969. On the mechanism of Langmuir circulations and their role in epilimnion mixing. Limnol. Oceanogr. 14: 493–503.

Simons, T. J. 1971. Development of numerical models of Lake Ontario, p. 654–669. *In* Proc. 14th Conf. Great Lakes Res., Int. Assoc. Great Lakes Res.

1972. Development of numerical models of Lake Ontario, Part 2, p. 655–672. *In* Proc. 15th Conf. Great Lakes Res., Int. Assoc. Great Lakes. Res.

1973. Comparison of observed and computed currents in Lake Ontario during Hurricane Agnes, June, 1972. *In* Proc. 16th Conf. Great Lakes Res., Int. Assoc. Great Lakes Res. (In press)

Stewart, R. W. 1969. Turbulence and waves in a stratified atmosphree. Radio Sci. 4: 1269–1278.

Stommel, H. 1970. Future prospects for physical oceanography. Science 168: 1531–1537.

Sundaram, T. R., and R. G. Rehm. 1971. Formation and maintainance of thermoclines in temperate lakes. Am. Inst. Aeronaut. Astronaut. J. 9: 1322–1330.

Sweers, H. E. 1969. Structure, dynamics and chemistry of Lake Ontario. Dep. Energ. Mines Resour. Mar. Sci. Br. MS Rep. Ser. No. 10: 227 p.

Thomas, R. L. 1972. The distribution of mercury in the sediments of Lake Ontario. Can. J. Earth Sci. 9: 636–651.

Tikhomirov, A. I. 1963. The thermal bar of Lake Lagoda. Bull. Izv. All-Union Geogr. Soc. 95: 134–142. (Am. Geophys. Union Transl. Sov. Hydrol.: Selected Pap. 1963–No. 2)

Turner, J. S. 1973. Buoyancy effects in fluids. Cambridge Univ. Press, Cambridge. 359 p.

Walin, G. 1972. On the hydrographic response to transient meteorological disturbances. Tellus 24(3): 169–186.

Woods, J. D. 1968. Wave induced shear instability in the summer thermocline. J. Fluid Mech. 32: 791–800.

Woods, J. D., and R. L. Wiley. 1972. Billow turbulence and ocean micro-structure. Deep-Sea Res. 19: 87–121.

Wu, J. 1969. Mixed region collapse with internal wave generations in a density stratified medium. J. Fluid Mech. 35: 531–544.

Zalkan, R. L. 1970. High frequency internal waves in the Pacific Ocean. Deep-Sea. 17: 91–108.

A Summary and Comparison of Nutrients and Related Water Quality in Lakes Erie, Ontario, Huron, and Superior[1]

HUGH F. H. DOBSON, MICHAEL GILBERTSON,[2] AND PETER G. SLY

Department of the Environment, Fisheries and Marine Service
Canada Centre for Inland Waters, Burlington, Ont. L7R 4A6

DOBSON, H. F. H., M. GILBERTSON, AND P. G. SLY. 1974. A summary and comparison of nutrients and related water quality in lakes Erie, Ontario, Huron, and Superior. J. Fish. Res. Board Can. 31: 731–738.

A summary is made, from recent data obtained by the Canada Centre for Inland Waters, of nutrients and water quality of offshore waters of the Great Lakes (excluding Lake Michigan). A simple indexing system, based on a limited number of variables, is used to describe related water quality.

DOBSON, H. F. H., M. GILBERTSON, AND P. G. SLY. 1974. A summary and comparison of nutrients and related water quality in lakes Erie, Ontario, Huron, and Superior. J. Fish. Res. Board Can. 31: 731–738.

Des données récentes, obtenues du Centre canadien des eaux intérieures, ont servi de base au présent résumé sur les substances nutritives et la qualité des eaux du large des Grands lacs (à l'exclusion du lac Michigan). On se sert d'un système d'indexage simple, basé sur un nombre limité de variables, pour décrire la qualité de l'eau.

Accepted January 21, 1974

To condense the wealth of existing data to manageable proportions and to simplify comparison, we have used mean values of selected variables in surface waters from a number of offshore sampling locations. Distributions of such variables throughout each lake are not discussed.

For those not familiar with the Great Lakes it may be pertinent, at this point, to provide some general statistics about their size. Lake Superior, at the head of the system, has an area of 82,410 km^2; its maximum depth is about 406 m and its mean depth about 148 m. Lake Huron and Georgian Bay have a combined area of 59,600 km^2, a maximum depth of 229 m, and a mean depth of 59 m. Lake Michigan's dimensions are similar to those of Lake Huron and Georgian Bay. Lake Erie has a surface area of 25,400 km^2 but has a maximum depth of only 64 m, with a mean of 18 m. Lake Ontario, the smallest of the Great Lakes, has an area of 18,800 km^2 and depths comparable to those of Lake Michigan. Lake Superior has the largest volume, about 12,000 km^3; Lake Erie has the smallest volume, about 540 km^3. For further details of the character and form of the Great Lakes, see Beeton and Chandler (1966), and Hutchinson (1957).

In this paper, we have considered, first, the presence of dissolved nutrient elements; nitrogen as nitrate and ammonia, phosphorus as inorganic phosphate or soluble reactive phosphate, silicon as reactive silicate and carbon as inorganic carbon; and dissolved organic matter.

The second part is concerned with the significance of Secchi depth, chlorophyll *a*, particulate phosphate, and dissolved oxygen, and the use of such data in conjunction with nutrient data as a means of indexing Great Lakes water quality.

Dissolved Nutrients

NITROGEN

Figure 1 shows the winter overturn values and late summer values for all lakes of nitrogen in the form of nitrate and ammonia (Lake Erie is subdivided into three basins), as a summary of the nutrient content of Great Lakes surface waters. Nitrogen values in winter are similar in most of the basins, about

---

[1] This paper, part of a special issue that comprises a comprehensive review of Limnology in Canada, was prepared to mark the 19th Congress of the International Association of Limnology (SIL), in Winnipeg, Man., during August 1974.

[2] Present address: (M.G) Canadian Wildlife Service, Floor 17, Place Vincent Massey, Hull, Que.

Printed in Canada (J3285)

200 µg N/liter. Lake Erie, however, peaks at about 640 µg N/liter in May. This inorganic combined nitrogen is not depleted much in summer in lakes Superior and Huron; however, summer values in lakes Erie and Ontario approach zero and this implies that shortages could be affecting phytoplankton.

Figure 2 illustrates differences between winter and summer values of nitrogen (as nitrate and ammonia), but the western basin of Lake Erie is excluded because it lacks a comparatively regular seasonal cycle. The increasing nitrogen metabolism, between lakes Superior and Ontario, is clearly reflected by the successive bar values (Superior 53 µg N/liter, Ontario 235 µg N/liter). Note that Lake Ontario appears to have twice the depletion shown in central Lake Erie (itself, twice as depleted as Lake Superior).

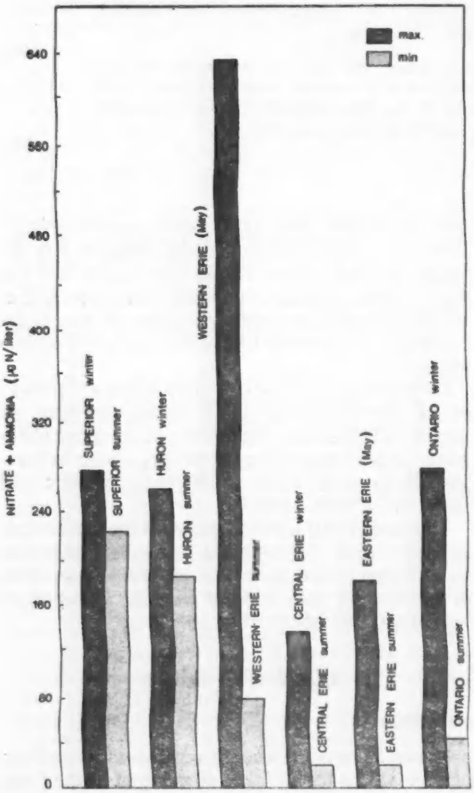


FIG. 1. Summary of nitrate + ammonia concentrations in surface waters of the Great Lakes, 1969–71 (from cruise-mean values at a depth of 1 m in each basin).

PHOSPHORUS

In Fig. 3 winter and summer values of dissolved inorganic phosphate or soluble reactive phosphate (Rigler 1968), are summarized. In lakes Superior and Huron, values remain low in winter and summer; this suggests that phosphate may well be a limiting factor for plankton growth in these two lakes. In lakes Erie and Ontario phosphate values are high in winter but low in summer; this suggests that, although eutrophic conditions may exist, phosphate depletion could, again, limit summer plankton growth.

In the case of nitrogen depletion, Lake Ontario metabolism is considerably more intense than that of Lake Erie and this is further borne out by the fact that Lake Ontario phosphate values are approximately twice those of central Lake Erie, in winter.

Figure 4 shows the difference between winter and summer reactive phosphate values for each of the lakes. In lakes Superior and Huron differences are undetectable, whereas lake Erie values are about 6 µg P/liter and Lake Ontario, 13 µg P/liter.

SILICON

Concentrations of reactive silicate in each of the lakes are shown in Fig. 5. In Lake Superior, values remain high in both winter and summer, suggesting that silicate is not a limiting factor

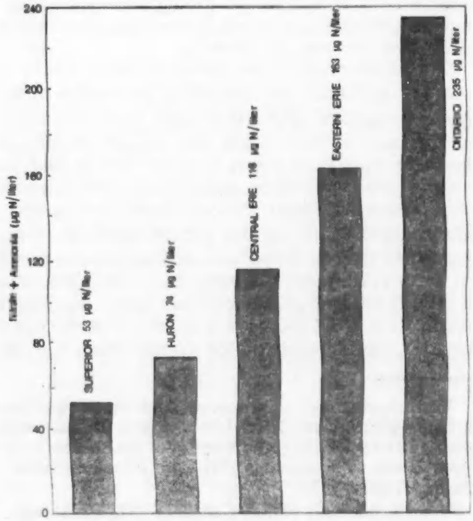


FIG. 2. Nitrate + ammonia in surface waters of the Great Lakes, 1969–71: winter maximum minus summer minimum. Units are µg N/liter.

there for the diatom fraction of phytoplankton production. In Lake Huron, values also are high in both winter and summer (though less than in Lake Superior). In lakes Erie and Ontario, however, winter values are already low and summer values approach zero; this strongly suggests that diatom growth is suppressed during summer by a lack of silicate.

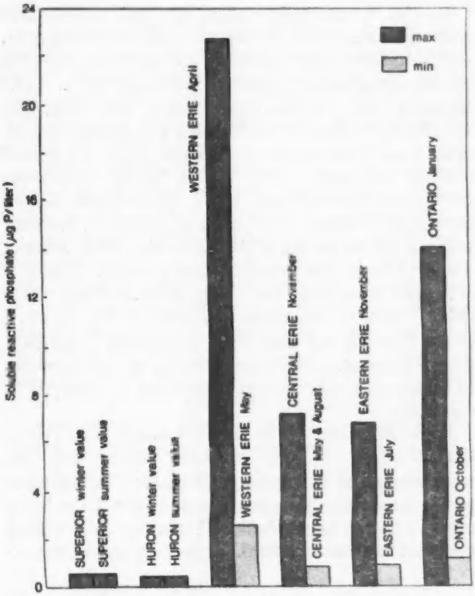


FIG. 3. Summary of soluble reactive phosphate concentrations in surface waters of the Great Lakes, 1969–71 (from cruise-mean values at a depth of 1 m in each basin.)

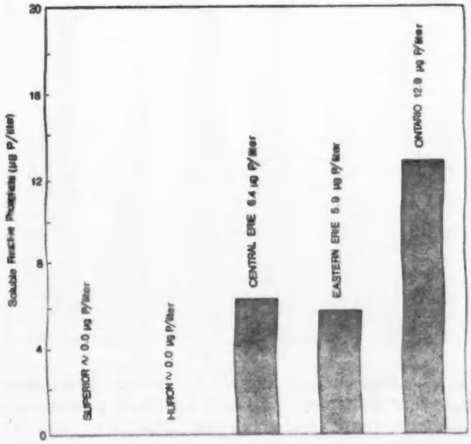


FIG. 4. Soluble reactive phosphate in surface waters of the Great Lakes, 1970: winter maximum minus summer minimum. Units are µg P/liter.

Differences between winter and summer values of dissolved (reactive) silicate, shown in Fig. 6, reflect the intensity of silicate metabolism, the uptake in surface waters during the spring, and replenishment from below during the autumn overturn. Mean values for 1969–71 indicate that Lake Superior had 210 µg SiO_2/liter, Lake Huron 536 µg SiO_2/liter, central Lake Erie 311 µg SiO_2/liter, eastern Lake Erie 276 µg SiO_2/liter, and Lake Ontario 330 µg SiO_2/liter. The anomalously high value in Lake Huron suggests abundant diatoms during an early stage of "eutrophication". Futher evidence of possible long-term depletion of dissolved silicate in Lake Huron may be found in Dobson (1971), and for Lake Michigan in Schelske and Stoermer 1971).

CARBON

Carbon may be considered as alkalinity, as most dissolved inorganic carbon is in the bicarbonate form. On such a basis, carbon-as-alkalinity can be reported for the Great Lakes as follows: Superior

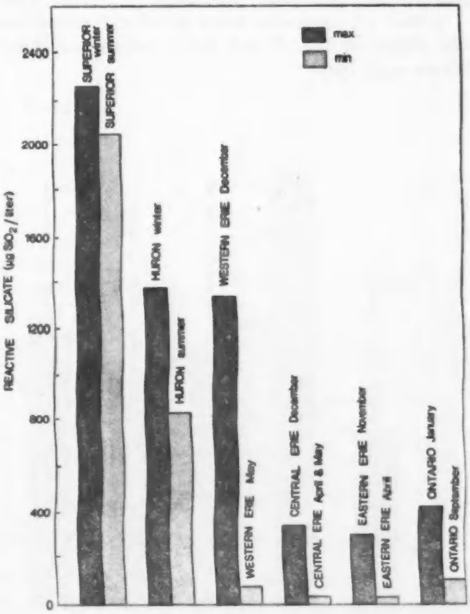


FIG. 5. Summary of reactive silicate concentrations in surface waters of the Great Lakes, 1969–71 (from cruise-mean values at a depth of 1 m in each basin).

10.0 μg C/liter, Huron 18.0 μg C/liter, all Erie basins 22.6 μg C/liter, and Ontario 22.6 μg C/liter.

As it is likely that phytoplankton can successfully utilize this source and as such alkalinity is little depleted in summer, the availability of dissolved carbon does not appear to be an important growth limiting factor.

DISSOLVED ORGANIC MATTER

This constituent has been deduced indirectly, in the form of dissolved organic phosphate, by subtraction, as the resultant of total dissolved phosphate less soluble reactive phosphate. A summary of dissolved organic phosphate in each lake is shown in Fig. 7. The three values for each lake and basin represent: 1, the mean value for surface waters of the cruise with the maximum value; 2, the grand mean value for the ice-free period; and 3, the mean value for surface waters of the cruise with the minimum value. From this figure it can be seen that the highest group values occur in lakes Erie and Ontario, but Lake Superior clearly has the lowest group values. Based on a comparison with total phosphate data (H. F. H. Dobson unpublished data), it appears that dissolved organic phosphate makes up about one-half the total phosphate present in the Great Lakes.

Values of measured total dissolved phosphate are shown in Fig. 8 and mean values are noted above each bar.

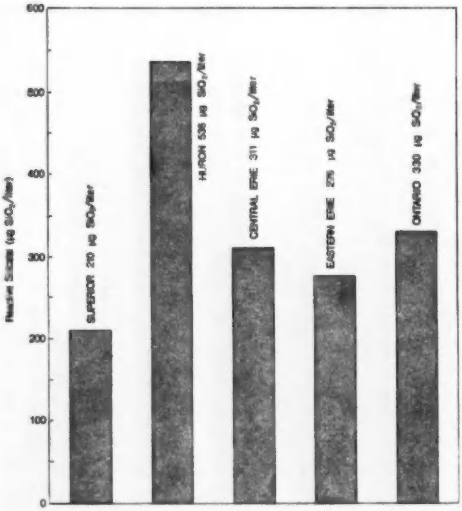


FIG. 6. Reactive silicate in surface waters of the Great Lakes, 1969–71; winter maximum minus summer minimum. Units are μg SiO_2/liter.

Particulate Fraction and Dissolved Oxygen

SECCHI DEPTH

In Fig. 9, smoothed values are used to illustrate mean annual curves of Secchi depth measurements, obtained from approximately monthly cruises made in the Great Lakes between 1969 and 1971. (Lake Superior and Huron cruises were less frequent.) On the right side of the diagram a nonlinear Secchi scale is used; on the left side a linear Secchi reciprocal scale is used (30/SD $m^{-1} \times 30$). Secchi reciprocals have been demonstrated to be approximate indicators of particulate matter, such as plankton, detritus, and suspended sediment (Vollenweider 1960; Postma 1961) if suspended mud is not present. Figure 9 is further separated into "oligo, meso, and eutrophic fields" based on separation bands at 3.0 m and 6.0 m SD. These bands have been established from data drawn from lakes Erie and Ontario, but a discussion of techniques used in this derivation is deferred at this time.

High $30/_{SD}$ values in western Lake Erie reflect the influence of both plankton counts and the resuspension of inorganic particulate; this is similar to the situation that occurs in southern Lake Winnipeg, another large shallow basin (G. J. Brunskill personal communication). Lower $30/_{SD}$ values in

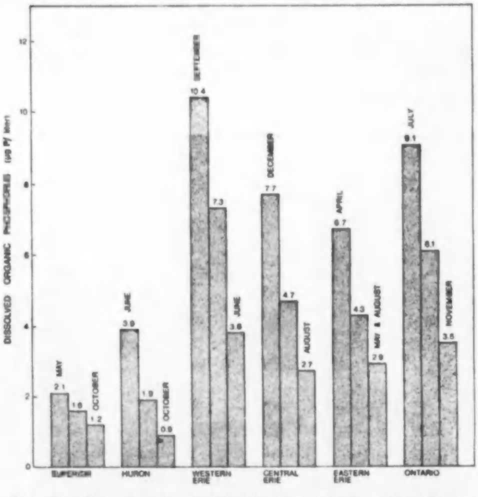


FIG. 7. Summary of dissolved organic phosphorus in surface waters of the Great Lakes. The indicated maximum, mean, and minimum values are those of the basin-wide mean values observed on monthly cruises in the ice-free period. Years of observation were: Lake Superior and Lake Huron, 1971, Lake Erie 1970, and Lake Ontario 1971 and 1972.

summer probably reflect reduced turbulence as well as changes in the productivity cycle.

The lowest $30/_{SD}$ values, which relate to Lake Superior, show almost no change throughout the annual cycle.

The annual curve for Lake Huron, although also exhibiting low $30/_{SD}$ values, is significantly different to that of Superior. In particular, the spring peaking and subsequent summer clearing (though not severe) are in marked contrast to the nondeviant values of Lake Superior.

The most interesting aspect of Fig. 9, however, lies in the opposing signature of the Lake Ontario curve, which shows a pronounced increase in $30/_{SD}$ values from June to October, with a well-formed peak in August. As most of the spring runoff into Lake Ontario is finished by mid-June and further, as the spring contribution of particulates from Lake Erie has also reached a maximum before mid-June, there appears to be little evidence of a significant contribution to any part of this peak in the form of locally derived inorganic particles. It may be assumed, threfore, that the curve for Lake Ontario relates principally to productivity.

CHLOROPHYLL *a*

Recent total chlorophyll *a* measurements on Great Lakes surface waters are shown in Fig. 10, and for comparative purposes a mesotrophic range (4.4 to 8.8 µg/liter has been provided. As noted in the previous discussion on Secchi depths, it is not intended to detail the establishment of these values at this time. The cruise-mean values for chlorophyll *a* across each lake surface through ice-free periods were examined and the maximum, grand-mean, and minimum values are illustrated as bar graphs.

Only lakes Superior and Huron remain wholely within the authors' "oligotrophic field," and western Lake Erie shows the highest recorded chlorophyll *a* maximum of 25.4 µg/liter. The central and eastern basins of Lake Erie and Lake Ontario show essentially similar chlorophyll *a* concentration values, though eastern Erie has the lowest maximum and grand-mean, and Ontario the lowest minimum. Chlorophyll *a* values for central and eastern Lake Erie and Lake Ontario span both the authors' "oligotrophic and mesotrophic fields."

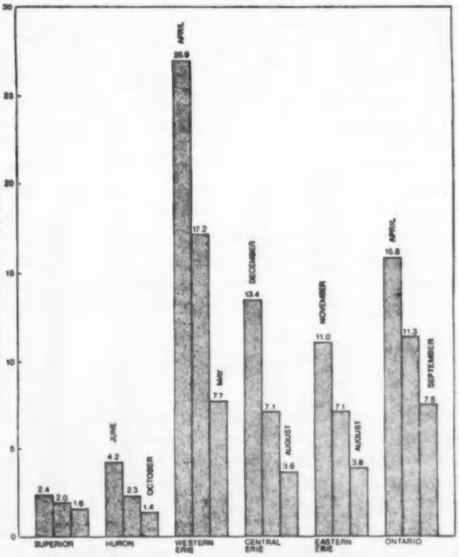


FIG. 8. Summary of total dissolved phosphorus in surface waters of the Great Lakes. The indicated maximum, mean, and minimum values are those of the basin-wide mean values observed on monthly cruises in the ice-free period. Years of observation were: Lake Superior and Lake Huron 1971, Lake Erie 1970, and Lake Ontario 1971 and 1972.

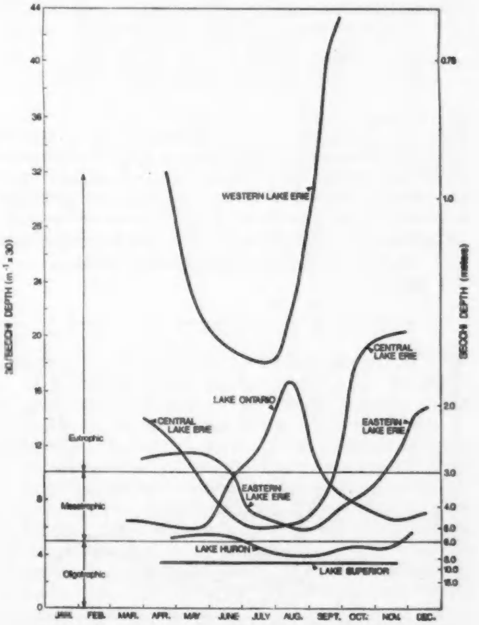


FIG. 9. Seasonal cycles of turbidity in surface waters of the Great Lakes, as indicated by the parameter 30/Secchi depth (m⁻¹). The smoothed curves were drawn from data obtained on synoptic cruises by CCIW from 1969 to 1971.

In Fig. 11 Secchi reciprocals and normalized chlorophyll *a* values are compared. A factor of × 1.14 has been used to correspond both sets of data to a common mesotrophic range of 5.0–10.0 $30/_{SD}$ (as previously utilized by the authors). Deviation between the two curves in the early spring, but more particularly during the winter (November, December), is ascribed to the influence of turbulent conditions and suspended inorganic particulates, and also to the lack of thermal stratification.

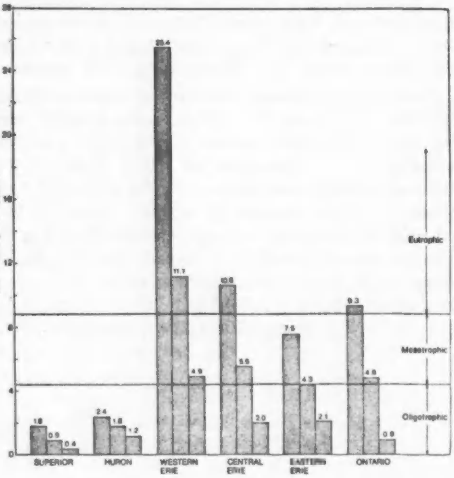


FIG. 10. Summary of total chlorophyll *a* concentrations in surface waters of the Great Lakes. The indicated maximum, mean, and minimum values are those of the basin-wide mean values observe on monthly cruises in the ice-free period. Years of observation were: Lake Superior 1968–71; Lake Huron 1971; Lake Erie and Ontario 1970. The mesotrophic range is 4.4–8.8 µg/liter.

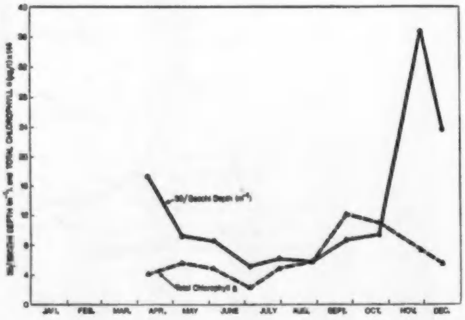


FIG. 11. Comparison of seasonal cycles of 30/Secchi Depth (m^{-1}) and total chlorophyll *a* in central Lake Erie during 1970, showing that turbidity is largely not associated with phytoplankton in spring and autumn.

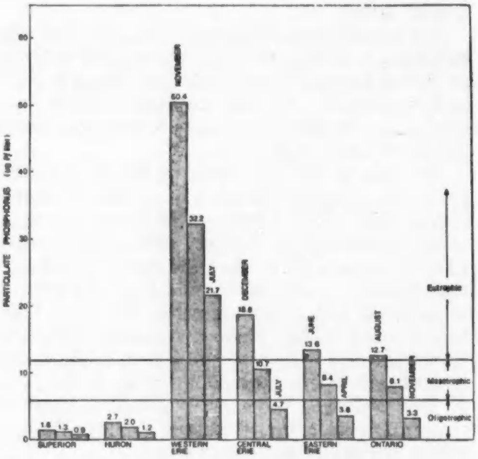


FIG. 12. Summary of particulate phosphorus concentrations in surface waters of the Great Lakes. The indicated maximum, mean, and minimum values are those of the basin-wide mean values observed on monthly cruises in the ice-free period. Years of observation were: Lake Superior and Lake Huron 1971, Lake Erie 1970, and Lake Ontario 1971 and 1972. The mesotrophic range is 5.9–11.8 µg P/liter.

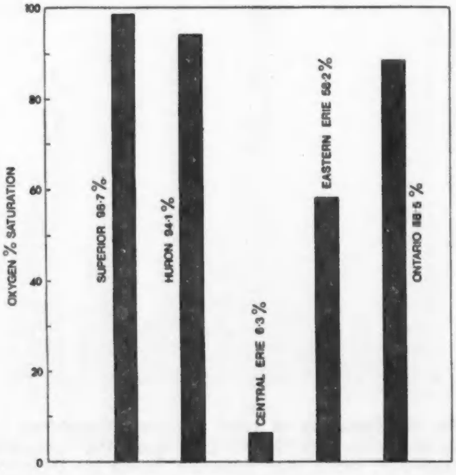


FIG. 13. The lowest cruise-mean oxygen % saturation values in hypolimnions of the Great Lakes during summer stratification, 1969–70.

PARTICULATE PHOSPHATE

Particulate phosphate values of the surface waters of each lake are illustrated in Fig. 12. These values were obtained by subtracting measured values of total dissolved phosphate from those of total phosphate as measured in unfiltered samples. The general distribution of values compares with those shown for chlorophyll *a* in Fig. 10. Particulate phosphate values are again stated in terms of maximum, grand-mean, and minimum of values obtained on cruises during ice-free periods. Lake Superior values range from 1.6 μg P/liter to 0.9 μg P/liter; similar but slightly higher values occur in Lake Huron. Western Lake Erie, however, exhibits at all times extreme values of from 50.4 μg P/liter to 21.7 μg P/liter. Although both the central and eastern basins of Lake Erie and Lake Ontario have maxima in excess of the authors' "upper mesotrophic field" boundary, the grand-means lie within the "mesotrophic field."

DISSOLVED OXYGEN

In Fig. 13, oxygen conditions in the hypolimnion waters of each lake, near the end of summer-stratification, are summarized. Values of less than 50% dissolved oxygen saturation are known to be hazardous to fish. Central Lake Erie, with dissolved oxygen values close to zero, is clearly in poor condition; further, the eastern basin with values of about 58% is also in a most unsatisfactory condition, particularly if it should continue to receive significant nutrient enrichment in future. However, Lake Ontario, with its high levels of nutrients in winter and abundance of phytoplankton in August, has no serious oxygen deficiency. This reflects a combination of circumstances possible in deep lakes (Hutchinson 1957, chapter 9).

Conclusions

From evidence presented, both lakes Superior and Huron are essentially oligotrophic, although the increasing productivity in Lake Huron (with its seasonal variations) suggests that it is moving significantly towards a mesotrophic state. The central and eastern basins of Lake Erie and Lake Ontario exhibit eutrophic symptoms but they are generally mesotrophic in the character of their water quality. The western basin of Lake Erie is eutrophic. Oxygen conditions in all the Great Lakes, with the exception of Lake Erie, are satisfactory. The western basin of Lake Erie is known to become anoxic under periods of calm summer weather, and the central basin has exhibited sustained periods of anoxic hypolimnion conditions in late summer.

Were it not for oxygen diffusion from the "reserves" in deep Lake Ontario, the high nutrient levels and productivity of this lake would effect degraded water quality conditions analogous to those now observed in Lake Erie.

Apparently definable trends in Great Lakes water quality (related to nutrient levels, turbidity, productivity, and dissolved oxygen) can be established on the basis of integrated and gross mean values. Techniques employed by the authors have utilized surface water mean values of the cruise with the maximum value (of *x*), the grand-mean value for the ice-free period, and the mean value for the cruise with the minimum value (of *x*), for nutrients; smoothed annual turbidity, and chlorophyll *a* curves; and dissolved oxygen percent saturation in the hypolimnion at the end of summer stratification. To index these trends the following values are likely required: nitrogen (as nitrate and ammonia), total phosphate and total dissolved phosphate and dissolved inorganic phosphate (soluble reactive phosphate), soluble reactive silicate, Secchi depth (or $30/_{SD}$), chlorophyll *a*, and dissolved oxygen percent saturation (Lake Erie hypolimnion).

Acknowledgments

We gratefully acknowledge the help and assistance of our colleagues at CCIW. In particular, we thank the water-quality chemists who made possible the interpretation of existing data. For further details on analytical methods, refer to Philbert and Traversy 1973.

The Director, CCIW, Mr J. P. Bruce, is acknowledged for permission to publish this material.

BEETON, A. M., AND D. C. CHANDLER. 1966. The St. Lawrence Great Lakes, p. 535–558. *In* D. G. Frey [ed.] Limnology in North America. The University of Wisconsin Press, Madison, Wis.

BURNS, N. M., AND C. ROSS. 1972. Project Hypo — an intensive study of the Lake Erie central basin hypolimnion and related surface water phenomena. Can. Centre Inland Waters, Paper No. 6; U.S. Environ. Prot. Agency Tech. Rep. TS-05–71–208–24.

DOBSON, H. H., AND M. GILBERTSON. 1971. Oxygen depletion in the hypolimnion of the central basin of Lake Erie, 1929 to 1970. Proc. 14th Conf. Great Lakes Res., p. 743–748.

HUTCHINSON, G. E. 1957. A treatise on limnology. Vol. 1, Geography, Physics and Chemistry. John Wiley and Sons, New York, N.Y. 1015 p.

POSTMA, H. 1961. Suspended matter and Secchi disc visibility in coastal waters. Neth. J. Sea Res., 1: 359–390.

RIGLER, F. H. 1968. Further observations inconsistent with the hypothesis that the molybdenum blue method measures orthophosphate in lake water. Limnol. Oceanogr. 13: 7–13.

VOLLENWEIDER, R. A. 1960. Beiträge zur Kenntnis Optischer Eigenschaften der Gewässer und Primä produktion. Mem. Ist. Ital. Idrobiol. Dott Marco de Marchi Pallanza Italy 12: 201–244.

A Comparative Review of Phytoplankton and Primary Production in the Laurentian Great Lakes[1]

R. A. VOLLENWEIDER, M. MUNAWAR, AND P. STADELMANN

Department of the Environment
Canada Centre for Inland Waters, Burlington, Ont. L7R 4A6

VOLLENWEIDER, R. A., M. MUNAWAR, AND P. STADELMANN. 1974. A comparative review of phytoplankton and primary production in the Laurentian Great Lakes. J. Fish. Res. Board Can. 31: 739–762.

Species composition of phytoplankton in the Laurentian Great Lakes, its biomass concentration, and its physiological activity measured as photosynthesis related to eutrophication, are reviewed and discussed.

VOLLENWEIDER, R. A., M. MUNAWAR, AND P. STADELMANN. 1974. A comparative review of phytoplankton and primary production in the Laurentian Great Lakes. J. Fish. Res. Board Can. 31: 739–762.

Les auteurs passent en revue et analysent la composition spécifique du phytoplancton des Grands lacs laurentiens, la concentration de sa biomasse et son activité physiologique mesurée comme photosynthèse liée à l'eutrophisation.

Accepted January 21, 1974

THE Laurentian Great Lakes occupy a unique position in the development of Canada and the United States and could be considered as presenting one of the most complex water management problems. During the past decades, there has been an enormous population increase in the Great Lakes Basin resulting in the accelerated eutrophication of these water bodies. Effects of eutrophication can be traced by the study of phytoplankton and its productivity. This paper deals with the species composition of phytoplankton, its biomass concentration, and its physiological activity measured as photosynthesis related to eutrophication.

Several review articles are available about phytoplankton (Davis 1966, 1969) and primary production (Saunders 1964; Verduin 1972). This paper reviews the present state of knowledge about the Great Lakes and emphasizes the Canadian contributions which were lake-wide, year-round, and more comprehensive. Although it concentrates on studies conducted at the Canada Centre for Inland Waters since 1967, research conducted by other agencies and universities of Canada and United States is included.

Phytoplankton Communities and Biomass

SCOPE, PROBLEMS, AND METHODS IN PHYTOPLANKTON STUDIES OF THE LAURENTIAN GREAT LAKES

Qualitative and quantitative knowledge of the organisms growing in an ecosystem is of fundamental importance. Quantification of these organisms provides an approximate measure of "biomass," which may be defined as "the living matter of the various groups of organisms present in an ecological sector at the time of observation." For phytoplankton, several biomass parameters have been used in limnological research; a schematic summary of the most commonly used ones with their relative merits is shown in Fig. 1. The problem of achieving some comparability of biomass by either biochemical or biological procedures has not been satisfactorily solved; each technique is plagued with analytical difficulties, assumptions, and hence, ambiguities. Biochemical determinations of phytoplankton biomass are impaired by the presence of detrital material, particulate inorganic material, zooplankton, and bacteria. Microscopic techniques (taxonomic identification and enumeration) are faced with at least two difficulties: (a) selection of proper microscopic techniques and counting procedures, and (b) availability of trained taxonomists to carry out the laborious work of identification and enumeration. The selection of proper microscopic techniques is of vital importance. If the objective of a research program calls for total phytoplankton biomass, one has to select a method such as Uter-

---

[1] This paper, part of a special issue that comprises a comprehensive review of Limnology in Canada, was prepared to mark the 19th Congress of the International Association of Limnology (SIL), in Winnipeg, Man., during August 1974.

Printed in Canada (J3287)

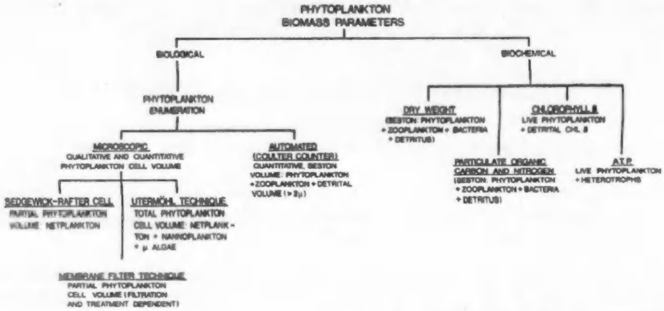

PHYTOPLANKTON BIOMASS PARAMETERS
BIOLOGICAL
BIOCHEMICAL
PHYTOPLANKTON ENUMERATION
MICROSCOPIC
QUALITATIVE AND QUANTITATIVE PHYTOPLANKTON CELL VOLUME
AUTOMATED (COULTER COUNTER)
QUANTITATIVE, SESTON VOLUME: PHYTOPLANKTON +ZOOPLANKTON + DETRITAL VOLUME (> 2μ)
SEDGEWICK-RAFTER CELL
PARTIAL PHYTOPLANKTON VOLUME: NETPLANKTON
UTERMÖHL TECHNIQUE
TOTAL PHYTOPLANKTON CELL VOLUME: NETPLANKTON + NANNOPLANKTON + μ ALGAE
MEMBRANE FILTER TECHNIQUE
PARTIAL PHYTOPLANKTON CELL VOLUME (FILTRATION AND TREATMENT DEPENDENT)
DRY WEIGHT
(SESTON: PHYTOPLANKTON + ZOOPLANKTON + BACTERIA + DETRITUS)
CHLOROPHYLL a
LIVE PHYTOPLANKTON + DETRITAL CHL a
PARTICULATE ORGANIC CARBON AND NITROGEN
(SESTON: PHYTOPLANKTON + ZOOPLANKTON + BACTERIA + DETRITUS)
A.T.P.
LIVE PHYTOPLANKTON + HETEROTROPHS

FIG. 1. Schematic summary of phytoplankton biomass parameters (from Munawar unpublished data.)

möhls (1958) which gives all components including net plankton (>64 μ), nannoplankton (<64 μ), and microalgae (< 5μ).

Little is known about the phytoplankton biomass and its composition in the Laurentian Great Lakes. This is surprising because the phytoplankton biomass and its composition in general, and certain species in particular, are perhaps the best indicators of water quality and trophic condition of a lake. Plankton investigations in the Great Lakes have been reviewed by Davis (1966, 1969); obvious deficiencies in earlier studies and certain major problems are as follows: a) No year-round studies were made; the past work was of a short-term nature and did not cover seasonal variation. b) Few lakewide cruises were carried out and thus, most of the studies were regional or localized. c) Inadequate and diverse techniques of preservation, concentration, and enumeration of phytoplankton were used, resulting in noncomparability of the Great Lakes data and with phytoplankton studies carried out in other parts of the world. d) Cell numbers of phytoplankton were not converted to biomass (cell volume or fresh weight); sometimes only the net plankton was reported, assuming it to be the dominant type of plankton. e) Too much emphasis was given to diatoms and blue-green algae (as net hauls or sedgwick Rafter cells were used); the qualitative and quantitative importance of other groups of algae such as phytoflagellates (Chrysomonadinae, Cryptomonadinae, and Dinophycinae) did not receive sufficient attention; the significance of nannoplankton and microalgae was completely neglected.

To remedy these deficiencies, a research program was initiated in 1967 at the Fisheries Research Board of Canada, Canada Centre for Inland Waters, Burlington, Ontario. Chlorophyll *a* surveys were started first, to obtain basic information about phytoplankton abundance. Later, phytoplankton and zooplankton enumeration and primary production measurements were included. The information regarding the phytoplankton biomass and its species composition of the Great Lakes given below has been extracted from papers by Munawar consisting of published and unpublished material.

PHYTOPLANKTON BIOMASS AND SPECIES COMPOSITION IN LAKE ONTARIO

Biomass — Among previous investigators, Nalewajko (1967, 1968) provided important information about Lake Ontario phytoplankton. The phytoplankton biomass and its species composition were investigated extensively from January to December, 1970 (Munawar and Nauwerck 1971).

Mean surface densities of phytoplankton biomass are given in Fig. 2 along with mean concentration of total (uncorrected) chlorophyll *a*. Biomass values ranged between 1.4 and 5.9 × 10^3 mg/m^3. Differences between inshore and offshore regions are apparent. The midlake region is characterized by lower densities of algae. Considerably higher concentrations were observed: 1) near St. Catharines, the Welland Canal, Niagara River, and Sodus Bay in the south; and 2) near Toronto, Oshawa, Murray Canal, Bay of Quinte, and most of the Kingston Basin in the north.

Except for some patchiness, the average chlorophyll *a* distribution also shows a more or less similar inshore to offshore pattern. Highest average concentrations of chlorophyll *a* (7–8 mg/m^3) were observed near St. Catharines, Rochester, and Sodus Bay on the southern shore of the lake, and near Toronto, Oshawa, and Bay of Quinte on the northern shore, as well as in the Kingston Basin. However, compared to average biomass distribution, a few discrepancies should be noted. For example, the average chlorophyll *a* concentration near Rochester, N.Y., is quite high (7 mg/m^3), but average biomass was very low ($<1.5 \times 10^3$ mg/m^3). A similar inconsistency existed also for the region between Toronto and Oshawa. Highest average phytoplankton biomass ($>4.5 \times 10^3$ mg/m^3) has been calculated for the southeastern basin near Oswego, N.Y., but chlorophyll *a* concentration does not support the biomass results.

Seasonal variations of mean phytoplankton biomass is given in Fig. 3. Only one well-developed peak of biomass occurs, in the middle of August,

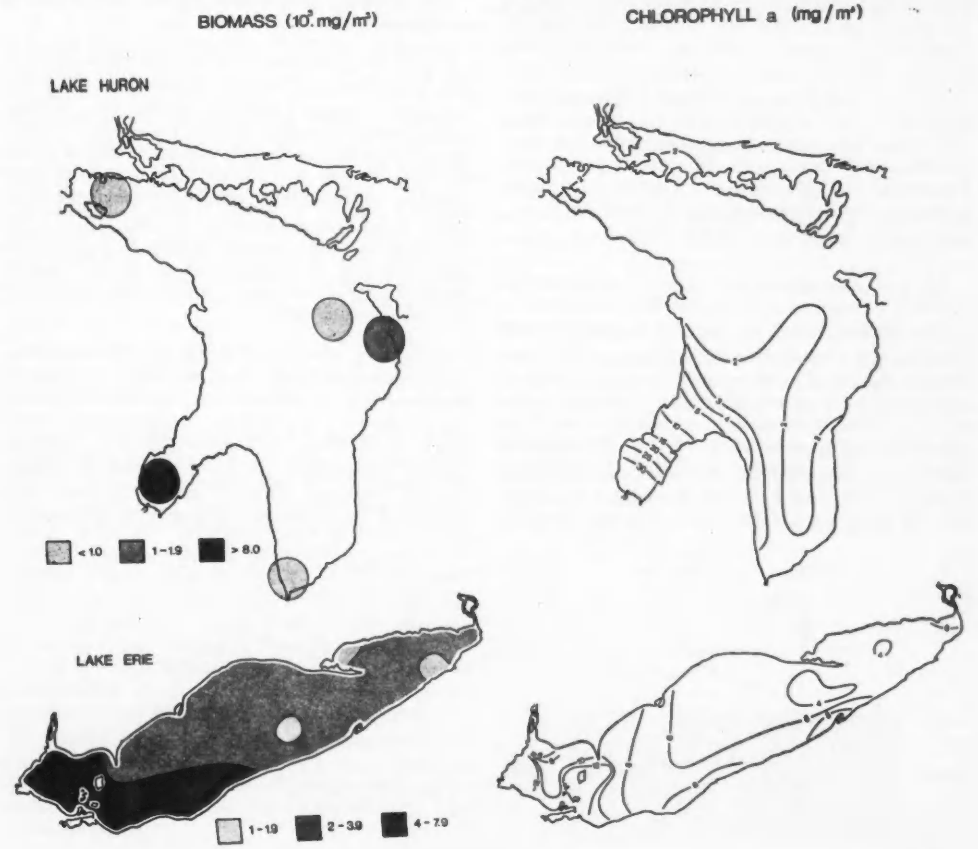

BIOMASS (10^3 mg/m^3)
CHLOROPHYLL a (mg/m^3)
LAKE HURON
< 1.0
1 – 1.9
> 8.0
LAKE ERIE
1 - 1.9
2 - 3.9
4 - 7.9
LAKE ONTARIO
< 1.5
1.5 - 2.5
2.5 - 3.5
3.5 - 4.5
> 4.5

FIG. 2. Mean surface distribution of phytoplankton biomass (cell volume) and chlorophyll *a* in lakes Ontario, Erie, and Huron during 1970 and 1971 (from Munawar and Nauwerck 1971; Munawar unpublished data).

and the average biomass during November to June ranged between 1 and 2 × 10^3 mg/m^3. The summer maximum was about four times this value.

Seasonal variation of total chlorophyll *a*, also given in Fig. 3, shows an interesting discrepancy with the fluctuations of phytoplankton biomass. These two variables were generally similar during the winter, spring, and fall periods when diatoms dominated the phytoplankton community (see below). However, during summer the biomass values showed a pronounced peak, whereas chlorophyll *a* showed significantly lower values, when green and blue-green algae dominated the community. This discrepancy is not explained yet, but could be attributed to incomplete pigment extraction for different species, nutrient deficiency, and species composition (Daley 1971).

Species composition and seasonal successions — A limited number of species were reported in earlier studies; based on live and Lugol-preserved samples, the investigations of Munawar and Nauwerck (1971) and A. Nauwerck (unpublished data) enlarged the list of identified algal species to some 360. In winter and spring the diatoms were responsible for approximately 90% of the biomass. The summer and fall phytoplankton showed more diversity, with green and blue-green algae contributing the most on a lake-wide basis; the diatoms, cryptomonads, and greens, in that order, were the most important constituents of the plankton. The phytoflagellates (not reported earlier) contributed considerably, sometimes comprising as much as 30% of the biomass (Munawar and Nauwerck 1971; Munawar 1973).

The detailed year-round species succession is described briefly by seasons:

a) Winter species — During the winter, species like *Scenedesmus bijuga* var. *irregularis* G.M. Smith was most common among the green algae. *Asterionella formosa* Hassall, *Diatoma elongatum* (Lyngb.) Ag. and *Surirella angustata* Kg. were typical winter diatoms. During the winter, phytoflagellates were found in large numbers, mainly *Rhodomonas minuta* Skuja and *Cryptomonas erosa* Ehrnb. A few other cryptomonads were usually present in the samples but were less common, such as *Sennia parvula* Skuja, *Katablepharis ovalis* Skuja, and *Cryptaulax rhombiodea* Nauwerck.

b) Spring species — The spring phytoplankton was dominated by diatoms, consisting of *Melosira Binderana* Kg. *M. varians* C.A. Agardh, *M. islandica* spp. *helvetica* O. Müller, *Stephanodiscus tenius* Hust., *S. Hatzschii* var. *pusilla* Grun, *S. Niagarae* Ehrnb., *Asterionella gracillima* (Hantzsch.) Heib., and *A. formosa*. Distinct spring blooms were developed by *Melosira Binderana*, *Stephanodiscus*

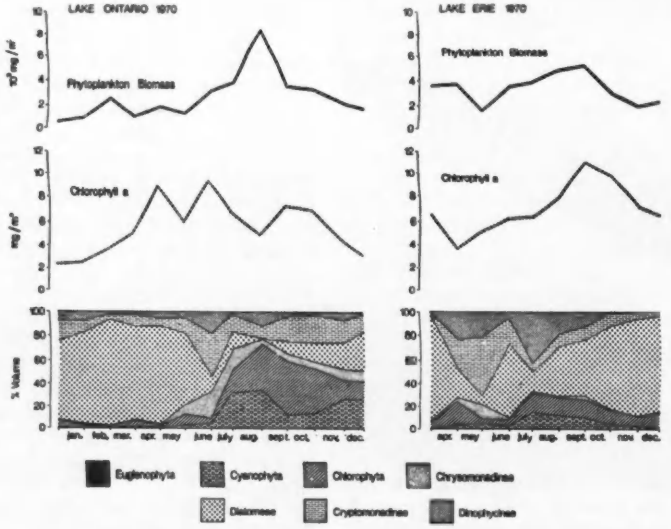


FIG. 3. Seasonal variations of surface phytoplankton biomass, its taxonomic composition, and chlorophyll *a* in lakes Ontario and Erie during 1970 (from Munawar and Nauwerck 1971; and Munawar et al. 1973).

tenuis, and *S. Hantzschii* var. *pusilla*. During spring the green algae were composed of species such as *Scenedesmus bijuga* var. *irregularis*, *Chlorella* spp., and *Coelastrum* microposum Naeg. Spring phytoflagellates had a composition similar to that observed during the winter.

c) Summer species — The summer phytoplankton was dominated by bluegreens like *Chroococcus dispersus var. minor* G. M. Smith and *Oscillatoria limnetica* Lemm. The greens were common and consisted of *Chlorella* spp., *Pedinomonas minutissima* Skuja, *Ankistrodesmus* falcatus var. *spirilliformis* G. S. West, *Oocystis Borgei* Snow, *Scenedesmus bijuga*, *Actinastrum Hantzschii* Lagerheim, and *Pediastrum simplex* (*Meyer*). Several colorless chrysomonads were found in the samples during June and July along with *Chrysochromulina parva* Lackey, which was commonly observed. During the summer, certain other species such as *Dinobryon sociale var. Americanum* (Brunth.) Bachm., *Rhodomonas minuta*, *Cryptomonas erosa*, *Katablepharis ovalis*, and species of *Gymnodinium* and *Glenodinium* were observed in small numbers.

d) Fall species — During the fall, the phytoplankton community was composed of Cyanophyta such as *Chroococcus dispersus* var. *minor* G. M. Smith, *Oscillatoria limnetica* Lemm., and Chlorophyta such as *Chlamydomonas globosa* Snow, *Pedinomonas minutissima*, *Chlorella* spp. *Ankistrodesmus falcatus* (Corda) Ralfs, *Oocystis Borgei*, *Coelastrum microporum*, and *Oedogonium* sp. The fall phytoplankton showed very few diatoms. Phytoflagellates belonging to Chrysomonadinae and Cryptomonadinae appeared frequently in considerable numbers. *Chrysochromulina parva*, *Rhodomonas minuta*, *Cryptomonas erosa*, and *Katablepharis ovalis* were the main components; *Chrysochromulina parva* in particular developed dense populations. The dinoflagellates were represented by *Gymnodinium helveticum* Penard and *Glenodinium* sp.

Certain species such as *Chroococcus dispersus* var. minor, *Chroococcus minutus* Kg. (Naeg.), *Ankistrodesmus falcatus* var. *spirilliformis*, *Scenedesmus bijuga*, *Rhodomonas minuta*, *Cryptomonas erosa*, and *Katablepharis ovalis*, were found year-round.

Inshore–offshore differentiation — Munawar and Nauwerck (1971) found that throughout the year four peaks of biomass were observed in the inshore region, whereas the offshore region had only one pulse. They also found that the pronounced spring maxima appeared in the inshore region only, and that the average biomass of the inshore region was about 25% greater than that of the offshore region. Diatoms dominated during the winter–spring period in both regions but their abundance in the inshore region was overriding. (Fig. 4).

In the inshore region, the March peak consisted mainly of *Stephanodiscus tenius*, *S. Hantzschii* var. *pusilla*, *Asterionella formosa* Hassall, and *Melosira varians* C. A. Agardh. Another pulse was observed during May at relatively high water temperature with different species dominated by *Melosira Binderana* Kg., with *Asterionella gracillima*, *Stephanodiscus tenius*, and *Melosira varians* as codominants.

However, in the offshore region typical inshore species such as *Melosira Binderana*, *Stephanodiscus tenius*, and *S. Hantzschii* var. *pusilla* were found in small numbers only; offshore communities were dominated by *Melosira islandica* spp. *helvetica* O. Müller. (M. Munawar, I. F. Munawar, and R. A. Vollenweider unpublished data).

Other inshore–offshore differences were observed in other seasons. For example, the inshore region showed two peaks of bluegreens, in summer and late fall, respectively, consisting of *Oscillatoria* spp. and *Chroococcus dispersus* var. *minor*. The offshore region showed only one summer pulse of bluegreens of similar species composition. As a whole, the offshore region harbored more greens

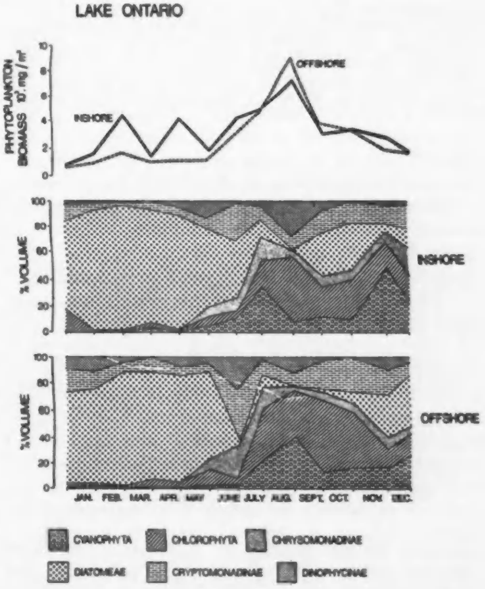


FIG. 4. Inshore and offshore differences of phytoplankton biomass and its composition in Lake Ontario during 1970 (Munawar 1973).

and phytoflagellates during the summer and fall seasons.

Other biomass variables — One of the problems of biomass measurements, whether microscopic or biochemical, is the difficulty of distinguishing between live and dead cells. There is a need to determine various biomass variables simultaneously, like ATP, chlorophyll *a*, particulate organic carbon, and cell volume, to judge their relative merits. An attempt was made during the studies of the International Field Year for the Great Lakes (IFYGL) (P. Stadelmann unpublished data) to determine the biomass by ATP determination of particulate matter using the method described by Holm-Hansen (1972). As an example, typical profiles of ATP, together with total particulate organic carbon, chlorophyll *a*, and photosynthesis rates, are presented in Fig. 5. At the offshore station high ATP concentrations occurred between 1 and 10 m, and particulate organic carbon and chlorophyll *a* reached their maximum between 15–20 m. The maximum value of ATP agreed with the maximum photosynthesis rate at 1 m.

At the inshore station, ATP, particulate organic carbon, chlorophyll *a*, and photosynthesis rates were similar in the euphotic zone, with maxima between 3 and 5 m depth. ATP concentrations were converted to "living" organic carbon using a C/ATP ratio of 250 (Holm-Hansen 1972); the "living" portion of particulate organic carbon of the integrated water column of 20 m depth varied from 5 to 65% and 6 to 25% at the offshore and inshore stations, respectively. Highest values were obtained in summer and lowest in winter.

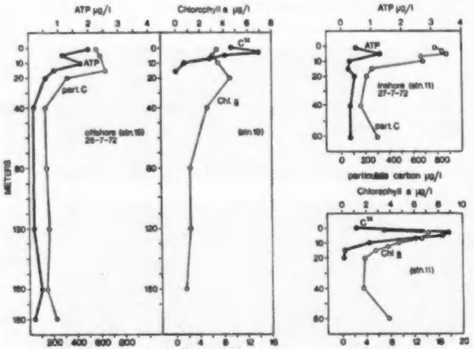


FIG. 5. Vertical profiles of ATP, total particulate organic carbon, and chlorophyll *a* (corrected) and photosynthesis rates in Lake Ontario at an offshore station (station 19) and inshore station (station 11) during IFYGL (July 1972) (Stadelmann unpublished data).

PHYTOPLANKTON BIOMASS AND SPECIES COMPOSITION IN LAKE ERIE

Biomass — Studies of the phytoplankton of Lake Erie, on a lake-wide basis, have been lacking until recently Munuwar et al. (1973). The Western Basin has received the most attention (Tiffany 1934; Chandler 1940, 1942, 1944; Verduin 1951, 1952, 1960, 1964; Wright et al. 1955; Casper 1965; Wujeck 1967; Hohn 1969; Olive et al. 1969; Taft and Taft 1971). Burkholder's (1929a, 1929b, 1960) and Davis's (1954a, 1954b, 1964, 1965) studies of the Central Basin are mainly based on nearshore waters. The studies of Braidech et al. (1971) extend to five stations in the Central Basin (part of project HYPO). Similarly, little is known about the phytoplankton of the Eastern Basin, but a few studies date back to the last century (Kellicot 1878; Mills 1882). Burkholder (1929a, 1929b, 1960), Gottschall (1930), and Gottschall and Jennings (1933) have made further contributions.

The average surface distribution of phytoplankton bomass and average total chlorophyll *a* is given in Fig. 2. Highest densities of phytoplankton biomass occurred in the Western Basin and some parts of the South Central Basin (4–7.9 × 10^3 mg/m^3).

The prevailing distribution pattern of chlorophyll *a* is similar to that of phytoplankton biomass. High average chlorophyll *a* values are clearly related to population centers and are in good agreement with the high biomass and nutrient concentrations (Gächter et al. 1974).

Seasonal abundance of surface phytoplankton and its composition on a lake-wide basis is given in Fig. 3. Maxima were recorded during spring and late summer. However, the average biomass remained relatively high during July–September. The spring peak was dominated by diatoms, phytoflagellates, and green algae. In May samples phytoflagellates were quite abundant, reducing the importance of diatoms significantly. The summer phytoplankton was mainly composed of dinoflagellates, cryptomonads, greens, and bluegreens. During this period diatoms were low in numbers, but they dominated again in the fall. On a lake-wide basis, abundance of bluegreens was not extensive, but they developed in larger concentrations in the Western Basin. Also, phytoflagellates played a more important role in Lake Erie than in Lake Ontario.

The total chlorophyll *a* followed the seasonal variations shown by the phytoplankton biomass, with a few exceptions in May and June.

Species composition and seasonal successions — From the lake-wide survey carried out in 1970, some 250 algal species have been identified. Of these, Chlorophyta made up some 60%, followed by Diatomeae (~10%), Dinophycinae (~10%), and Chrysomonadinae (~5%), and the rest from other groups. The number of species identified were 148, 144, and 150 in the Western, Central, and Eastern basins, respectively.

The seasonal succession can be described as follows:

a) Spring species — During spring (April onward) the community was composed of diatoms, phytoflagellates, and green algae. Common species (>5% of total biomass) of diatoms were *Asterionella formosa, A. gracillima, Tabellaria flocculosa, Fragilaria crotonensis, F. capucina, Stephanodiscus tenuis, S. Hantzschii var. pusilla, S. Niagarae, Melosira islandica,* and *Melosira Binderana,* and among the green algae were *Chlamydomonas globosa, Chlorella* spp., *Oocystis Borgei, Coelastrum microporum, Pediastrum duplex, Schroedaria judayi, Actinastrum Hantzschii,* and species of *Scenedesmus.* The phytoflagellates (Chrysomonadinae, Cryptomonadinae, and Dinophycinae) were dominated by *Ochromonas* spp., *Chrysochromulina parva, Rhodomonas minuta, Cryptomonas erosa, Cryptomonas* spp., *Katablepharis ovalis, Gymnodinium helveticum, G. uberrimum, Gymnodinium* spp., *Glenodinium* sp., and *Peridinium aciculiferum.*

b) Summer species — The summer phytoplankton was mainly composed of phytoflagellates, greens, and bluegreens. Common phytoflagellates were cryptomonads like *Rhodomonas minuta, Cryptomonas erosa, Katablepharis ovalis,* dinoflagellates like *Gymnodinium* sp., *Glenodinium* sp., *Ceratium hirundinella* which was most abundant during the summer period. Species like *Chlamydomonas globosa, Oocystis Borgei, Coelastrum microporum, Coelastrum* spp., *C. cambricum, Pediastrum simplex, P. boryanum, P. duplex, Pediastrum* spp., *Gloeocystis* spp., *Sphaerocystis* sp., *Staurastum paradoxum, Mougeotia* sp., *Oedogonium* sp., and *Cosmarium* sp. were representative for the green algae. The blue-green algae were essentially composed of *Chroococcus dispersus* var. *minor, Aphanocapsa* spp., *Anabaena spiroides,* and *Aphanizomenon flos aquae.*

c) Fall species — In contrast to the summer plankton, diatoms like *Asterionella formosa, A. gracillima, Fragilaria crotonensis, F. capucina, Stephanodiscus tenuis, S. Niagarae,* and particularly *Coscinodiscus Rothii* (a marine species) dominated the fall communities.

Comparison between the basins — The discussion in the previous section gives an overall picture of seasonal variations of phytoplankton communities on a lake-wide basis, and is useful for comparisons of the lakes; however, it does not provide a sufficient picture of the variability in the three basins of Lake Erie. In fact, the east–west differentiation is considerable, and probably exceeds the inshore–offshore differentiation.

To preserve a synthetic presentation, a summary picture of the three basins is given in Fig. 6 in which each basin is treated as a unity. Although this treatment smooths the north–south differentiation, particularly in the Central Basin, it characterizes the extent of similarity or dissimilarity of the three basins in regard to biomass production and seasonal group composition.

The highest biomass was found in the Western Basin, showing essentially two seasonal peaks, one in early spring with average values of 13 × 10^3 mg/m^3, and a slightly lower one in August with 8 × 10^3 mg/m^3. In contrast to this, no comparable spring peak was found in the Central and Eastern basins. The Central Basin reached its biomass maximum in late summer (about 6 × 10^3 mg/m^3), whereas in the Eastern Basin several maxima of the same order of magnitude (about 4 × 10^3 mg/m^3) were observed.

In regard to biomass production and its seasonal cycles, the three basins are therefore essentially dissimilar. These dissimilarities are also reflected in dissimilarities in the seasonal composition of the phytoplankton communities; however, certain features are more common to at least two basins, whereas others are not. For example, the Western and Central basins are more similar in the succession and relative importance of diatoms during all seasons, whereas in the Eastern Basin diatoms are practically absent from the plankton communities over a 3-mo period from June to August. Conversely, in regard to dinoflagellates, the Central and Eastern basins are similar, but both differ from the Western Basin. Phytoflagellates taken as a whole (chrysomonads, cryptomonads, dinoflagellates, however, show a definite gradient, becoming progressively more important community components from west to east. Chlorophyta are important components of the spring and early summer plankton in the Western Basin, but in the Eastern Basin they were abundant only in summer and fall; in the Central Basin they are present in modest amount throughout the year. Bluegreens reach a distinct maximum in late summer only in the Western Basin; in the Central and Eastern basins they never dominate the plankton communities but can be found over considerable periods of time.

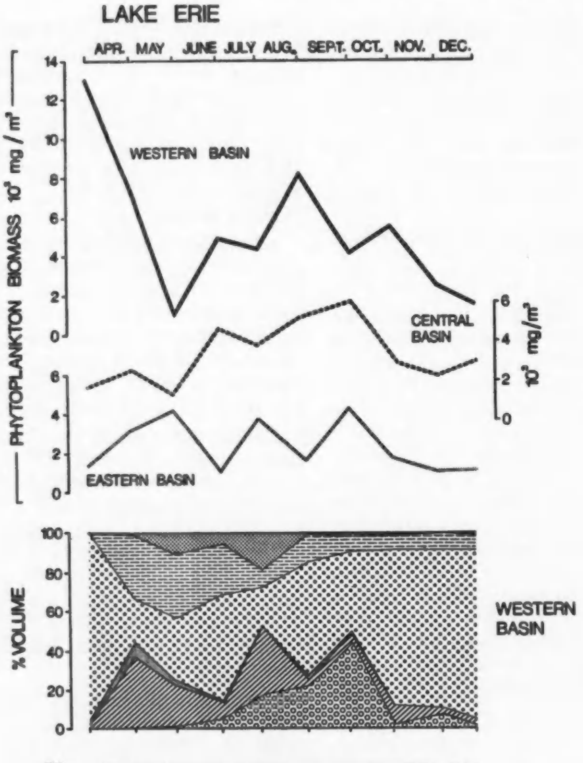


FIG. 6. Seasonal variation of surface phytoplankton biomass and its composition for Lake Erie basins during 1970 (M. Munawar and I. F. Munawar unpublished data).

Summing up, the salient differences between the three basins are as follows:

Western Basin — Diatoms were dominant most of the time. Greens and bluegreens were abundant during spring and summer. Phytoflagellates were common in spring.

Central Basin — Diatoms were dominant but less abundant during spring and summer. Bluegreens were considerably lower in concentration. Phytoflagellates were more abundant during spring, but they were also found in large numbers during summer.

Eastern Basin — Diatoms were dominant during the fall and were absent throughout the summer. Bluegreens were less abundant, but greens were common during the summer. Chrysomonads were most abundant in this basin. Phytoflagellates were most prevalent, encroaching on diatom growth.

No satisfactory explanation for this differentiation can be given at this time except for differences in total biomass, which of course are related to the different nutrient status of the three basins. Furthermore, a few of the features in algal group preponderance are related to this — for example, the large amount of bluegreens in the Western Basin — but it is not clear why they are of little relative importance in the Central Basin. However, the increasing relative importance of phytoflagellates from west to east reflects the decreasing trophic gradient in the same direction, but nevertheless may also be related to a west–east gradient in temperature and thermal stability.

Considering species composition, some species developed more frequently in one basin than in the other. For example, in the Western Basin *Aphanizomenon flos aquae* Ralfs was abundant, whereas its volume was low in the Central Basin. In the Eastern Basin its development was so low that it never contributed more than 5% to the total biomass. Another example is *Anabaena spiroides* var. *contracta*, which developed in both the Western and Central basins but seems to have flourished more in the Central Basin. Certain species were also characteristic in each basin, e.g. *Coscinodiscus Rothii* (E) Grun, *Actinastrum Hantzchii* Lagerh., and *Ceratium hirundinella* (O. F. Müller) Schrank were typical for the Western Basin. Species of *Ochromonas* and the dinoflagellate *Peridinium aciculiferum* Lemm. were most common in the Central Basin. The Eastern Basin was characterised by abundance of species of *Gymnodinium*, *Glenodinium*, and *Amphidinium* — particularly *Gymnodinium helveticum* and *G. uberrimum*.

Certain common species were perennial and occurred year round. In the Western Basin the perennial species were *Stephanodisus tenuis*, *Melosira islandica*, *M. Binderana*, *Fragilaria crotonensis*, and such cryptomonads as *Rhodomonas minuta* and *Cryptomonas erosa*. The perennial species of the Central Basin were *Ochromonas* spp., *Stephanodiscus Niagarae*, *Rhodomonas minuta*, and *Cryptomonas erosa*. The Eastern Basin harbored perennial species like *Pediastrum duplex*, *Fragilaria crotenensis*, *Rhodomonas minuta*, and *Cryptomonas erosa*.

COMPARISON OF LAKE ONTARIO AND LAKE ERIE

It is interesting to note that the average phytoplankton biomass values of lakes Ontario and Erie, when calculated on a lakewide basis, are not much different (2.7 and 3.4 × 10^3 mg/m^3, respectively). Further, the average inshore and offshore values of Lake Ontario are similar to those calculated for the Central and Eastern basins of Lake Erie, but both the inshore and offshore regions of Lake Ontario remain 25–50% below the average values of the highly productive Western Basin (Table 1).

In regard to phytoplankton composition, the two lakes are more conveniently compared season by season (Fig. 3). In Lake Ontario during winter, spring, and early summer, diatoms dominated the community overridingly, whereas in Lake Erie (only spring data are available) the importance of diatoms decreases during April as phytoflagellates increase (chrysomonads, cryptomonads, and dinoflagellates). Generally, however, the same succession can be observed in both lakes (diatoms → phytoflagellates → green and bluegreens) over the early part of the year with a phase difference of about 2 mo from Lake Erie to Lake Ontario (Fig. 3). During the 2nd half of the year, the dominance pattern is different in the two lakes. In Lake Ontario, the summer–fall–early winter plankton as a whole remains dominated by greens and bluegreens; in Lake Erie, diatoms regain importance only in the fall and definitively dominate the early winter plankton.

A comparative evaluation of succession patterns in relation to specific environmental conditions still awaits completion. This will be possible once the material from all lakes has been elaborated, and then there will be a basis for a comparative ecology of phytoplankton of the Great Lakes as a function of specific environmental variables such as temperature, mixing cycles, illumination, and nutritional status.

OTHER LAURENTIAN GREAT LAKES

Lake Huron — Extremely little has been published on the phytoplankton of Lake Huron. Fenwick (1962, 1968) has published some qualitative data,

TABLE 1. Mean values and range of surface phytoplankton biomass in lakes Ontario, Erie, and Huron.

	No. stations	Phytoplankton biomass $x10^3 \times$ mg/m^3		Remarks	Reference
		Mean	Range		
Lake Ontario	27	2.7	0.7–8.5	Jan.–Dec. 1970 13 cruises	
Inshore	7	3.3	0.8–7.4	" "	Munawar and Nauwerck (1971)
Offshore	20	2.6	0.6–9.0	" "	
Lake Erie	24	3.4	1.8–5.2	Apr.–Dec. 1970 10 cruises	
Western Basin[1]	5	5.3	0.8–13.2	" "	Munawar et al. (1973)
Central Basin	12	3.2	0.6–6.0	" "	
Eastern Basin	7	2.4	1–4.2	" "	
Lake Huron					
Mid-lake station	1	0.9	0.3–1.8	Apr.–Dec. 1971 8 cruises	Munawar and Munawar (1973)
Saginaw Bay station	1	8.3	1.6–17.3	" "	

and Parkos et al. (1969) have given a brief list of genera found during a short investigation period (July–August, 1968). Based on a C.C.I.W. survey covering the period April–December, 1971, some preliminary results can be reported Munuwar and Munuwar (1973).

The stations selected for these analyses were located in the south (near Sarnia, Ontario), mid-lake, northern and northeastern parts (near Bruce Peninsula), and in Saginaw Bay. Figure 2 shows the stations located near Sarnia, mid-lake, and the northern part of the lake exhibiting average biomass concentrations of less than 1.0×10^3 mg/m^3; the inshore stations off Bruce Peninsula and Saginaw Bay showed higher average values of 1.5 and 8.2 $\times 10^3$ mg/m^3, respectively. The highest mean values were observed in the eutrophic Saginaw Bay.

Mean concentration of total chlorophyll *a* was about 2 mg/m^3 in the open lake, whereas the eutrophic Saginaw Bay exhibited a high concentration (up to 30 mg/m^3).

Seasonal variation of phytoplankton biomass, composition, and total chlorophyll *a* is given in Fig. 7 for a mid-lake station and for a station in Saginaw Bay. The mid-lake station showed very low biomass concentration ranging from 0.3 to 1.7×10^3 mg/m^3. Total chlorophyll *a* was also low (0.8–4.5 mg/m^3). The phytoplankton biomass and chlorophyll *a* did not develop any pronounced peaks, as was observed for lakes Ontario and Erie. Diatoms dominated at the mid-lake station during the entire period of study (April–December). However, the total phytoflagellates belonging to Cryptomonadinae and Dinophycinae, hitherto unreported, contributed sometimes up to 20% of

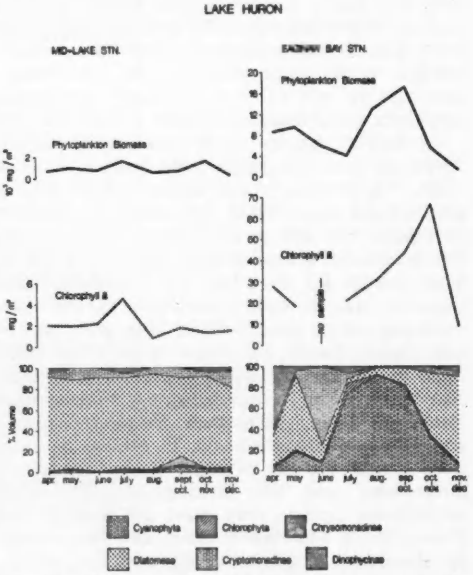


FIG. 7. Seasonal distribution of surface phytoplankton biomass and its composition at an offshore station of Lake Huron and at a station in Saginaw Bay during 1971 (Munawar and Munawar 1973).

the biomass. The diatoms were mainly composed of species of *Cyclotella*, *Tabellaria*, *Stephanodiscus*, *Melosira*, and *Synedra*. Species such as *Fragilaria crotonensis* and *Tabellaria fenestrata* were common in the samples. Various species of phytoflagellates were usually found in all the samples in low numbers and rarely contributed up to 5% of the biomass. Cryptomonads like *Rhodomonas minuta* and *Cryptomonas erosa* sometimes contributed up to 5–10% of the biomass. In Saginaw Bay the phytoplankton biomass ranged between 1.6 and 17.3 × 10^3 mg/m^3 (Fig. 7). These values are extremely high compared to those observed at the mid-lake station of Lake Huron. Biomass densities in Saginaw Bay are even higher than those observed in the Western Basin of Lake Erie (0.8–13.2 × 10^3 mg/m^3). A broad, long-lasting maximum developed from July until the end of September, dominated by bluegreens. However, during spring (May), a relatively dense population dominated by diatoms was observed.

Saginaw Bay was unique as far as algal composition was concerned. Diatoms played a significantly less important role compared to the mid-lake station. Bluegreens dominated the community most of the summer, with species such as *Chroococcus dispersus* var. *minor*, *Aphanocapsa* spp. *Gomphosphaeria* sp., *Oscillatoria* spp. *Anabaena spiroides*, and *Aphanizomenon flos aquae*. Also, phytoflagellates were abundant in Saginaw Bay compared to the mid-lake station. During June, *Cryptomonas erosa* and *Cryptomonas* spp. made up 75% of the biomass. Dinoflagellates were also found in higher concentration during April, consisting of *Peridinium aciculiferum*, *Gymnodinium uberrimum*, and *Gymnodinium* spp.

Total chlorophyll *a* also showed high values compared to values reported in the literature (9.2–66.6 mg/m^3). The seasonal patterns shown by phytoplankton biomass and total chlorophyll *a* were not identical. The biomass peak was observed earlier (September–October), whereas the chlorophyll *a* peak was observed a month later (October–November). Chlorophyll *a* showed a peak when bluegreens diminished in concentration and diatoms increased. This is another example of the observed discrepancy between biomass and chlorophyll *a*, similar to that observed in Lake Ontario (above).

Lake Superior — Since the review of Davis (1966) little has been published about the phytoplankton of Lake Superior. Parkos et al. (1969) gave some information about the genera found during 1967. Schelske et al. (1972) explored the effects of nutrient enrichment on phytoplankton productivity and species composition. A review of these early and recent studies indicates that our knowledge of the phytoplankton of Lake Superior is preliminary and limited to net plankton, especially diatoms. The present limited knowledge of Lake Superior phytoplankton is deplorable, as this lake is the most oligotrophic, and yet it has not been compared thoroughly with the other Great Lakes whose environments have already undergone qualitative and quantitative changes due to cultural eutrophication. Lake Superior has been the focus of an extensive lake-wide survey at the Canada Centre for Inland Waters and six monitor cruises were completed from April–December, 1973. The Great Lakes Biolimnology Laboratory at C.C.I.W. has collected samples at 55 stations to study the horizontal and vertical distribution of phytoplankton.

Some preliminary analyses of live and Lugol-preserved samples collected during 1971 and 1973 have been done. Analyses of spring and summer samples indicate that most stations show low phytoplankton biomass and that the algal populations are composed not only of diatoms but also of chrysomonads, cryptomonads, dinoflagellates, greens, and bluegreens.

Our recent lake-wide survey of chlorophyll *a* (H. F. Nicholson unpublished data) indicates that most of the open lake has values less than 1.0 mg/m^3. Higher chlorophyll *a* concentrations were observed near Whitefish Bay, Thunder Bay, and in the western basin of the lake (near Duluth).

Lake Michigan — Lake Michigan has received considerable attention recently and several reports have been published (Holland 1968, 1969; Holland and Beeton 1972; Stoermer et al. 1971, 1972; Stoermer and Yang 1970; Schelske et al. 1971; Ayers and Seibel 1973). However, most of these studies have dealt mainly with diatoms. Munawar, and Claflin and Beeton (unpublished data) using similar techniques (Utermöhl 1958) have found several phytoflagellates like *Chrysochromulina parva*, *Rhodomonas minuta*, *Cryptomonas erosa*, *Dinobryon cylindricum*, *D. sociale*, and *D. divergens*. Recently, Munawar has also analyzed a few samples from the southern end of Lake Michigan. His preliminary study indicated that diatoms were the dominant phytoplankton but phytoflagellates like *Rhodomonas*, *Cryptomonas*, *Katablepharis*, *Chromulina*, *Chrysochromulina*, and *Kephyrion* were commonly found.

Total chlorophyll *a* determinations were made by Robertson et al. (1971). They reported a range of 0.3–5.3 mg/m^3; the highest concentrations were found in the southern portion of the lake. Fee (1971) studied chlorophyll *a* on a five-station transect in Lake Michigan. He reported values ranging between 0.6 and 10.3 mg/m^3. From his studies, lake-wide average chlorophyll *a* concentration has been estimated as between 2 and 3 mg/m^3.

For comparison, the phytoplankton biomass and chlorophyll *a* concentrations of the Great Lakes are summarized in Table 1 and 2.

Primary Production

Problems and Reviews

Measurements of photosynthesis on large bodies of water such as the Laurentian Great Lakes are tedious and expensive. If in situ experiments are conducted, few stations can be investigated, and the results may not be representative of the whole lake. More photosynthesis data can be obtained by utilizing shipboard light incubators, but without in situ references it might be difficult to extrapolate such data to natural conditions. A well-balanced combination of in situ and incubator measurements, therefore, gives the most we can expect under such circumstances.

Direct measurements of photosynthesis in the Great Lakes were first performed during the period 1952–62 in western Lake Erie by Verduin (for review see Saunders 1964), followed by studies in Lake Michigan (Saunders et al. 1962; Saunders 1964) and Lake Superior (Putnam and Olson 1961; Olson and Odlaug 1966; Putnam and Olson 1966). These studies were limited to single stations and covered only certain periods of the seasonal cycle. From 1967 on, studies were carried out for longer periods and in larger areas of Lake Huron, Michigan, and Superior (Parkos et al. 1969; Schelske and Roth 1973).

Beginning in 1970, the Canada Centre for Inland Waters started a year-round, lake-wide program to investigate primary production in lakes Ontario and Erie; in 1971 it was extended to Lake Huron, and in 1973 to Lake Superior. Meanwhile, year-round studies on a representative transect of Lake Michigan were made by Fee (1971). Based on these and the previously mentioned investigations, an intercomparison of the Great Lakes with regard to primary production is possible for the first time, as similar experimental techniques were used by the various investigators — Parkos et al. conducting ^{14}C experiments using an incubator with constant light and temperature (9000 1x, 16 C), Fee exposing

TABLE 2. Mean range of chlorophyll *a* (mg C/m^3) in the Great Lakes (lakes Michigan and Superior values are not corrected for pheopigments).

	No. stations	Chlorophyll *a*		Remarks	Reference
		Mean	Range		
			Lake Ontario		
Inshore	10	5.2	2.7–12.0	Jan.–Dec. 1970 13 cruises	Glooschenko et al. (1972, 73, 74b)
Offshore	22	3.8	1.8–7.9	" "	
			Lake Erie		
Western basin	5	8.9	3.3–19.3	Apr.–Dec. 1970 10 cruises	" "
Central basin	12	4.4	2.5–9.2	" "	
Eastern basin	8	3.2	1.4–5.4	" "	
			Lake Huron		
Open lake	44	1.7	1.4–2.2	Apr.–Dec. 1971 8 cruises	" "
Saginaw Bay	2	16.9	9.5–27.4	" "	
			Lake Michigan		
	3	2.3	0.3–5.3	May–Nov. 1967 8 cruises	Robertson et al. (1971)
Inshore	2	–	1.1–10.3	May 1970–Feb. 1971	Fee (1971)
Offshore	3	–	0.6–3.7	16 cruises	
			Lake Superior		
	130	–	0.4–9.7	May–Aug. 1973	H. F. Nicholson (unpublished data)

^{14}C bottles in an incubator at four light intensities, and the C.C.I.W. study group using an incubator with constant light intensity (8000 1x for lakes Ontario and Erie, and 30,000 1x for lakes Huron and Superior), keeping temperature close to surface water temperatures. The C.C.I.W. incubator experiments were further supplemented on each cruise by at least one in situ experiment.

Hourly uptake rates per unit of volume at about light optimum obtained by these techniques are reasonably comparable. Yet different procedures were used by the three groups for calculating integral production: Parkos et al. based their calculations on previous in situ expositions performed by Putnam and Olson in 1961 at one station; Fee modified and applied Vollenweider's photosynthesis model based on actual irradiance (Vollenweider 1965); and the C.C.I.W. group extrapolated daily production, correlating incubator ^{14}C experiments with Secchi depth readings and in situ experiments (Glooschenko et al. 1974a). The C.C.I.W. results of 1970 for Lake Ontario have been corroborated in a subsequent intensive study of in situ production at two stations carried out by Stadelmann et al. (1974) during the IFGYL.

A summary of available results of hourly, daily, and integral photosynthesis rates from the abovementioned studies is given in Table 3; these values may also be compared to a corresponding listing of phytoplankton biomass and chlorophyll *a* values (Table 1 and 2).

HORIZONTAL DIFFERENTIATION

As already mentioned, the Great Lakes show considerable horizontal differentiation in biomass, a feature that is also reflected at the primary production level.

Figure 8 represents the average primary production (mg C/m^3 per h) for lakes Ontario, Erie, and Huron, as found during the 1970–71 studies. In terms of hourly uptake rates, Saginaw Bay is by far the most productive area, exceeding that of western Lake Erie. The influence of Saginaw Bay on the open water can be traced far out to the Central Basin of the lake and south to Sarnia, but the main water body of Lake Huron is less productive than any large area of the other two lakes. In western Lake Erie the region of highest production extends on the south shore from Toledo to Sandusky, but the influence of the Western Basin on the Central Basin can be recognized on both the north and south shores. The abrupt change in isopleths beyond Bass, Pelee, and Kelley's islands is partly due to the prevailing flow direction of the Detroit River water from north to south in that region. Additional nutrient loads received by the Central Basin from Cleveland and Erie are also easily recognized in the primary production patterns.

In Lake Ontario, however, the average production pattern reflects only in part the influence of nutrient discharges from city outfalls such as Toronto, Hamilton, Rochester, and Oswego. The average pattern is determined mainly by the inshore–offshore differentiation and the phase difference in the production cycle in these two subregions of the lake. High production rates are found also in the Kingston Basin, which is not directly influenced by city discharges. The low production area in the main body of the lake is due to deep mixing over a prolonged period of time, and not primarily to scarcity of nutrients (Gächter et al. 1974; Stadelmann et al. 1974).

PRODUCTION CYCLE

Figure 9 summarizes production cycles for lakes Ontario and Erie found during the 1970 studies. In Lake Ontario, the inshore–offshore differentiation is more important than any other horizontal differentiation. Production rates in the inshore region reaches its maximum in April–May, when primary production rates are still in the ascending phase in the offshore region. From July to October no essential differences in activity exist between the two regions. The same cycles have been found by Stadelmann et al. (1974) who determined daily production rates based on in situ ^{14}C experiments (Fig. 10). In a somewhat finer breakdown, however, considering the lake station by station, several kinds of cycles in Lake Ontario could be distinguished on the basis of chlorophyll *a* variations: a unimodal cycle with a summer maximum in the deep waters of the western half of the lake; a bimodal pattern along the north and south shores and the central portion of the lake; a series of three or more pulses in the extreme western portion and the eastern third of the lake. The pluripulse behavior seems to be typical of areas relatively rich in nutrients, such as the Hamilton and Rochester areas (also Munawar and Nawerck 1971; Glooschenko et al. 1972).

Because of its morphology, the inshore–offshore differentiation in Lake Erie is less pronounced lakewide, though not negligible. There are, however, large differences in the cycles of the three basins. C.C.I.W. studies started after the ice break-up, but we believe that the first pulse usually begins in March under the ice-cover. In the Western Basin, a high phytoplankton biomass was found to be already present at the time of the first survey (see above), but during the same period assimilation activity was very low. In this basin three production peaks have been found, with a maximum in August, yet probably many more short pulses occur which

TABLE 3. Photosynthesis rates in the Great Lakes.

	Date	mg C/m^3/h	mg C/m^2/h		mg C/m^2/day	g C/m^2/yr	Reference
			Lake Ontario				
Inshore stations (10)	Jan.–Dec. 1970	2.9–25.0^{a}		27–110^{a}	120–1080^{a}	190(170)^{b}	Glooschenko et al. (1974a)
Offshore stations (22)	Jan.–Dec. 1970	1.7–12.4^{a}		17–100^{a}			” ”
Inshore station (1)	Apr.–Apr. 1972–73	–	1.8–26.7^{c}	11–184^{d}	119–2003^{d}	270^{d}	Stadelmann et al. (1974)
Offshore station (1)	Apr.–Apr. 1972–73	–	1.4–33.3^{c}	23–178^{d}	58–1443^{d}	170^{d}	” ”
			Lake Erie				
Eastern stations (8)	Apr.–Dec. 1970	3.2–13.9^{a}		15–120^{a}	140–1440^{a}	(160)^{b}	Glooschenko et al. (1974a)
Central stations (14)	Apr.–Dec. 1970	5.5–21.4^{a}		17–141^{a}	120–1690^{a}	(210)^{b}	” ”
Western stations (3)	Apr.–Dec. 1970	4.8–146.9^{a}		5–397^{a}	30–4760^{a}	(310)^{b}	” ”
			Lake Huron				
Stations (13–14)	May–Aug. 1968	4.9–12.0^{a}					Parkos et al. (1969)
Stations (40)	Apr.–Dec. 1971	2.2–9.9^{a}		21–63^{d}	147–698^{d}	100(80–90)^{b}	Glooschenko et al. (1973)
Saginaw Bay (2)	Apr.–Dec. 1972	4.1–127.2^{a}		–	–	–	” ”
			Lake Michigan				
Stations (17–24)	July–Oct. 1967	8.1–17.5^{a}		–	–	–	Parkos et al. (1969)
Northern stations (11–5)	July–Aug. 1969	2.5–4.1^{a}		–	–	–	Schelske and Callender (1970)
Offshore stations (3)	June–Feb. 1970–71	–	0.9–4.2^{c}	–	67–1030	121–139	Fee (1971)
Inshore stations (2)	June–Feb. 1970–71	–	1.4–30.1^{c}	–	67–1567	187–247	”
			Lake Superior				
Larsmont station (1)	July–Aug. 1961		0.25–0.73^{c}	–	183^{e}	–	Olson and Odlang (1966)
Stations (23–26)	July–Oct. 1967	2.6–8.8^{a}		–	185^{f}	–	Parkos et al. (1969)
Stations (20–22)	May–Aug. 1968	4.7–6.4^{a}		–		–	” ”
Stations (58)	July–Sept. 1973	2.2–2.7^{a}		32–35^{d}	330–350^{d}		C.C.I.W. (unpublished data)

[a] Mean of each cruise.

[b] During the investigation period.

[c] $P_{opt.}$

[d] In situ values.

[e] Maximum observed values.

[f] Mean of the two seasons.

are missed by monthly cruises, as evidenced by the LETS (Lake Erie Time Study) Project (Kramer et al. 1970).

In the Central Basin, a broad summer–fall maximum continues until October and is probably due to nutrient enrichment of the epilimnion from the hypolimnion during the initial overturn period (Gaechter et al. 1974). The production cycle in the Eastern Basin is smoother, having its maximum during summer.

Production cycles in lakes Huron and Superior have not yet been properly analyzed. From the C.C.I.W. studies in 1971 in Lake Huron, (Glooschenko et al. 1973) it would appear that photosynthetic activity during the growth season in the main body remains almost constant, exhibiting a small summer maximum. In contrast to this, Saginaw Bay seems similar to the Western Basin of Lake Erie, having several pronounced production maxima from spring to fall.

The production cycle of Lake Superior seems comparable to that of the open water body of Lake Huron, i.e. showing low variability over the growth season. Here also we may expect that local areas such as the extreme Western Basin and bays show a different picture.

VERTICAL DIFFERENTIATION AND DYNAMICS

The kind and extent of vertical differentiation in primary production is not well known because of difficulties connected with in situ primary production measurements in such large bodies of water. The few in situ measurements carried out on regular cruises gave vertical carbon uptake rate curves which, with a few exceptions, compare well with classical photosynthesis profiles, showing an assimilation optimum, the depth position of which varies depending on the optical properties of the water (Rodhe 1958; Vollenweider 1960). In Lake Ontario optimal depth varies from 1 to less than 10 m, whereas in the more transparent upper lakes, the optima may be found at depths below 10 m. Yet, on the basis of the few data available, no final comparison of the extent of the photic zone of the various lakes can be made at present.

The situation is better known for Lake Ontario through the time series studies carried out by Stadelmann et al. on two stations over a full year cycle. Two typical examples are given in Fig. 5.

This study shows that generally depth profiles are quite regular in this lake, with little dependence on stratification. Nevertheless, during the summer stratification period, a sophisticated analysis of the photosynthesis–light relation revealed the existence of physiologically differentiated populations along the vertical axis reacting differently to a variable light regime. Harris (1973) and Harris and Lott (1973a, b) approached a similar problem by considering the importance of vertical mixing. Combining in situ and laboratory studies of the physiological response of Lake Ontario phytoplankton to a variable light field, and computer-simulating photosynthesis profiles in a mixed water

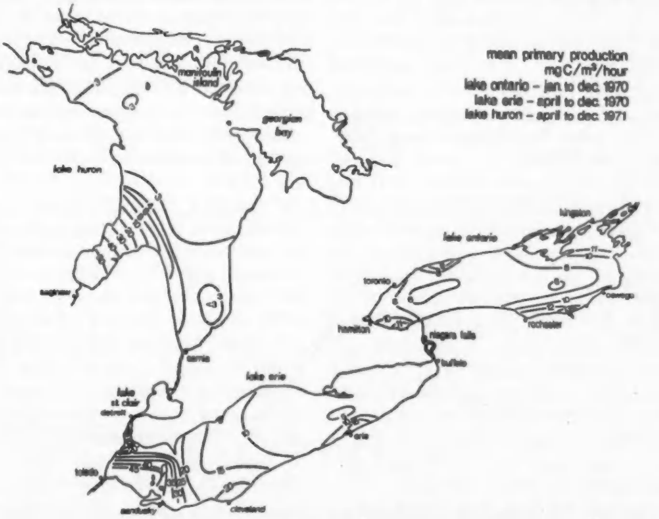

mean primary production
mgC/m³/hour
lake ontario – jan to dec 1970
lake erie – april to dec 1970
lake huron – april to dec 1971
manitoulin island
georgian bay
lake huron
saginaw
sarnia
lake st clair
detroit
toledo
sandusky
cleveland
lake erie
erie
buffalo
niagara falls
hamilton
toronto
lake ontario
kingston
oswego
rochester
3
<3
45
40
30
25
20
15
10
12
11
8

FIG. 8. Mean primary production rates for lakes Ontario, Erie, and Huron during 1970 and 1971 (from Glooschenko et al. 1973, 1974a).

column, they conclude that photoinhibition, as observed in static bottle experiments, is probably to a large extent suppressed in a dynamic natural situation of plankton moving vertically up and down. Accordingly, our estimates of primary production would be too low.

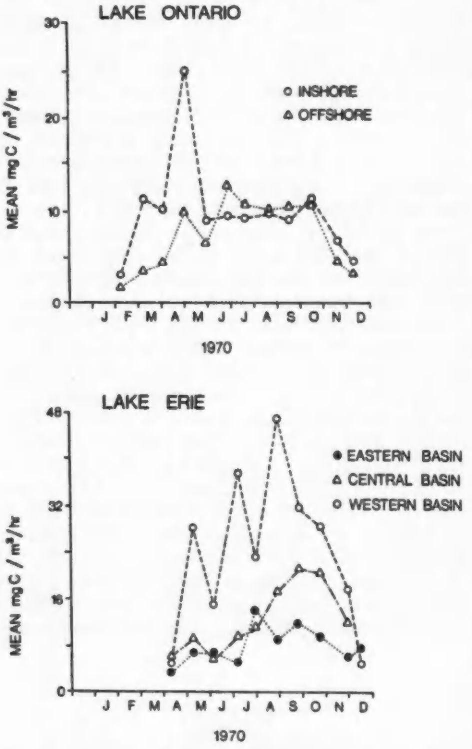


Fig. 9. Mean primary production in surface waters of Lake Ontario and Lake Erie basins during 1970 (from Glooschenko et al. 1974a).

The findings of Harris are of considerable importance for future primary production studies as a whole. At present their results cannot be applied properly to correct our estimates based on bottle techniques. However, this is of minor importance at this stage of research because the primary goal of our studies was to get comparable, rather than absolute, production rates.

Production–Biomass Relation

Relative assimilation activity (production/biomass quotients) of algal populations can be defined in several ways using various biomass variables, such as cell volume or fresh weight, chlorophyll *a*, particulate organic carbon, nitrogen, and ATP. Most commonly used quotients are: a) assimilation number: mg C_{ass}/unit of time per mg chlorophyll *a* at light optimum; b) activity coefficient; mg C_{ass}/unit of time per mg of biomass. As production rates are expressed in carbon units, it is convenient to use the same units for phytoplankton biomass. Algal volume or fresh weight can be converted approximately to organic carbon using a factor of 0.1 (Nauwerck 1963). The conversion of chlorophyll *a* to organic carbon is more difficult (Eppley 1972). The ratio of carbon to chlorophyll may vary with a factor of more than 9 (Parsons et al. 1961; Caperon and Meyer 1972). Various investigators based their conversion factors on different C/chlorophyll *a* ratios, e.g. 40 (Strickland 1960) and 100 (Holm-Hansen 1969). If both production rate and biomass refer to the same unit of habitat, the obtained P/B quotient has the unit $time^{-1}$ and gives information about carbon turnover rate.

Generally the turnover rate of carbon in an aquatic ecosystem can be determined for three

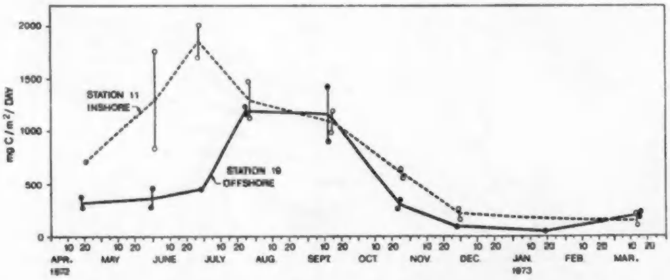


Fig. 10. Daily photosynthesis rates at an inshore and offshore station, Lake Ontario, during 1972–73 based on in situ experiments (from Stadelmann et al. 1974).

compartments: a) carbon turnover rate of phytoplankton; b) carbon turnover rate of living plankton; and c) carbon turnover rate of the seston (particulate organic material). To obtain the carbon turnover rate of phytoplankton, the values of fresh weight (cell volume) are converted to carbon. The living fraction of plankton material can be estimated by ATP determination of particulate material, which is converted to carbon using a factor of 250 (Holm-Hansen 1972). Total organic carbon content in the water can be measured directly by determination of particulate organic carbon.

Mean hourly assimilation numbers based on ^{14}C experiments and chlorophyll *a* determination (corrected for pheopigments) have been computed for lakes Ontario, Erie, and Huron (Glooschenko et al. 1973, 1974a). About 3 mg C/h per mg chlorophyll *a* were found for the most eutrophic regions of the Great Lakes (e.g. Saginaw Bay, Western Basin of Lake Erie). Lower numbers, 1–1.5 mg C/h per mg chlorophyll *a*, were generally found for mid-lake stations.

Activity coefficients have been computed recently by M. Munawar (unpublished data) using a factor of 0.1 to convert fresh weight to carbon for Lake Ontario. These mean volumetric carbon turnover rates varied between 0.02 to 0.1 and 0.02 to 0.2/h in inshore and offshore regions, respectively.

Hourly carbon turnover rates at light saturation were determined in Lake Ontario based on ATP determination. Values ranged from 0.03 to 0.27 and 0.08 to 0.28/h at the inshore and offshore stations, respectively. Corresponding turnover rates for total particulate organic carbon fluctuated between 0.01–0.04 and 0.01–0.05/h, respectively (P. Stadelmann unpublished data).

Some attempt could now be made to determine daily turnover rates of carbon. Taking an average daylight period of 10 h, the maximum volumetric carbon turnover rate of phytoplankton based on Munawar's activity coefficient are 1.0–2.0/day at the inshore and offshore regions, respectively. Comparing these values with those of Stadelmann, maximum carbon turnover rates for living plankton and total particulate organic carbon were 2.8 and 0.5/day, respectively. Highest turnover rates were obtained for living plankton and lowest for total particulate organic carbon; turnover rates for phytoplankton were intermediate. Carbon turnover rates of particulate organic carbon on an areal basis (m^2), considering a euphotic zone of 20 m, ranged between 0.04–0.18 and 0.01–0.21/day at the inshore and offshore stations, respectively (Stadelmann et al. 1974). This means that 1–21% of total organic carbon in the specified layer is renewed daily by photosynthesis.

ESTIMATES OF AVERAGE YEARLY PRIMARY PRODUCTION

Calculated values for yearly primary production are the least accurate because of the amplification of errors resulting from conversion of measured hourly values to daily and yearly estimates, and because of uncertainties about the relative proportions of areal and vertical differentiations. In full awareness of these problems, the values presented below are probably the best we can give at this time, and apparently they are no less reliable than many figures reported in the literature for lakes having more ideal conditions for global estimates of this sort.

Lake Erie, as a whole, is the most productive lake among the Great Lakes (Table 3). Estimates for April–December give values of 310, 210, and 160 g C/m^2 for the Western, Central, and Eastern basins, respectively. Yearly production values for these basins have to be increased by an estimated 10%, though the precise values may differ from basin to basin. Accordingly, yearly production of the three basins would be about 340, 230, and 175 g C/m^2/yr, respectively. Accounting for the relative size of the three basins (1:5:2), the average annual production of Lake Erie as a whole would be about 240–250 g C/m^2 per yr.

The annual average production of Lake Ontario is estimated to be 180–190 g C/m^2/yr (based on 1970 and 1972–73 studies) — probably as good an estimate as one can make for a lake of its size (Table 2). In fact, the estimates of Glooschenko et al. and of Stadelmann et al., respectively, obtained by different methods, are identical for any practical purpose. Also, the inshore–offshore differences (discussed above) are well reflected in the yearly estimates (270 and 170 g C/m^2 per yr, respectively).

Estimates for lakes Huron and Michigan are less satisfactory, though still representative. The lakewide average annual production of 80–90 g C/m^2 per yr for Lake Huron is probably of the right order of magnitude but needs better definition for the Saginaw Bay region, which is among the most productive areas of all the Great Lakes (Table 3). For Lake Michigan, the east–west differentiation is well documented by Fee's investigations, but the year-round north–south differentiation still needs to be studied. A first-order estimate for the whole lake, based on Fee's figures and accounting for relative extension of inshore to offshore areas, would give an average yearly production of 140–150 g C/m^2/yr.

The C.C.I.W. data for Lake Superior are still under elaboration, and it is difficult to give a good estimate of yearly production. If one takes the figures of Parkos et al. as representative for a 4–6-

mo growth season, and half of their values as representative for the rest of the year, the total annual production would be 40–50 g C/m² per yr. However, recent (1973) in situ measurements over a period comparable to that covered by Parkos et al. give almost twice the integrated daily production rates of those estimated in 1967 (Table 3). It cannot be said at this stage if this discrepancy is due to differences in methods, or reflects a real increase in production of Lake Superior over the last 5–6 yr; in fact, this latter cannot be ruled out a priori, but will be difficult to substantiate with any degree of certainty.

Trophic Status of the Laurentian Great Lakes

PRODUCTION IN RELATION TO NUTRIENTS

Seasonal cycles of the most important nutrients such as phosphorus, nitrogen, and silica for the C.C.I.W. study period in lakes Ontario and Erie are discussed by Gächter et al. (1974). Similar analyses are under way for the 1971 Lake Huron and the 1973 Lake Superior studies. Also, lakewide summaries (annual average concentrations, winter maxima, summer minima, and their differences) for all four lakes have been computed by Dobson et al. (1974). Nutrient loading estimates, in particular for phosphorus, are available from a variety of sources (IJC Reports 1969, 1973; Patalas 1972; Lee 1974).

Generally there is good agreement between yearly production and epilimnetic nutrient depletion during the summer stagnation of the four lakes. However, there are peculiarities worth mentioning. According to our estimates, the annual production of Lake Ontario and eastern Lake Erie is similar, yet the apparent nutrient depletion over the growth season for both nitrogen and phosphorus is considerably higher in Lake Ontario (for phosphorus almost 2:1), compared to eastern Lake Erie. Conversely, nitrogen depletion in the Central Basin is lower, and phosphorus depletion only slightly higher, than in the Eastern Basin, in spite of the higher annual production of the Central Basin compared to the Eastern basin. Silica depletion in lakes Superior, Erie, and Ontario is similar, but is double in Lake Huron. Similar discrepancies are also to be noted for hypolimnetic oxygen depletion rates. Therefore, the apparent metabolic activity of any of the principal nutritional variables is determined by a number of factors other than total production, such as lake morphology, epilimnion to hypolimnion ratio, flushing and residence time, etc.

Highly significant though nonlinear correlations have been found to exist between average particulate phosphorus, average chlorophyll *a*, annual primary production, and annual phosphorus loadings, indicating a high degree of consistency between the variables measured hitherto.

Average uncorrected chlorophyll *a* and average particulate phosphorus, expressed as mg/m³, are related by a parabolic function

$$\text{chlorophyll } a = 0.9 \times (\text{PP})^{0.75}$$

This relation is not necessarily representative if calculated on individual pairs of values over the seasons. A similar though less significant relation (because of some uncertainties relative to loading figures) has been found between average particulate phosphorus and annual total phosphorus loadings, i.e.

$$(\text{mg PP/m}^3) = 10 \, (\text{g TP/m}^2 \text{ per yr})^{0.6}$$

Further, it was possible to relate annual primary production (g C/m² per yr) to average particulate phosphorus by a function of the form $\frac{ax}{b+x}$, which corresponds to a generalized photosynthesis integral,

$$\Sigma a = F(i) \times \frac{\pi \times \text{P}}{\epsilon_w + \epsilon_\pi \text{P}}$$

(Vollenweider 1970; Megard 1972). The values of the variables in this last function cannot be estimated individually, but constants appearing in the global function have been determined as $a = 420$, and $b = 9$. Accordingly, the potential upper limit of annual production in the Great Lakes would be 420 g C/m² per yr, a value almost reached in the Western Lake Erie Basin (above).

On this basis, then, the relationship between annual production, average chlorophyll *a*, and annual phosphorus loadings, respectively, may be quantified as follows:

$$\Sigma \, a \, (\text{g C/m}^2 \text{ per yr}) = 420 \, \frac{1.15 \, (\text{mg chlorophyll } a/\text{m}^3)^{1.33}}{9 + 1.15 \, (\text{mg chlorophyll } a/\text{m}^3)^{1.33}}$$

$$\Sigma \, a \, (\text{g C/m}^2 \text{ per yr}) = 420 \, \frac{10 \, (\text{g TP/m}^2 \text{ per yr})^{0.6}}{9 + 10 \, (\text{g TP/m}^2 \text{ per yr})^{0.6}}$$

These relations, together with measured values, are represented in Fig. 11 and 12.

However, these relations, though highly significant for the lakes in question, cannot necessarily be applied to other Great Lakes. Such a generalization will be possible only on the basis of a much broader set of data. It is anticipated that correlations of the sort given above for the Great Lakes can be established for groups of lakes having comparable limnological properties, from which it may then be possible to deduce a generally valid relation of some sort.

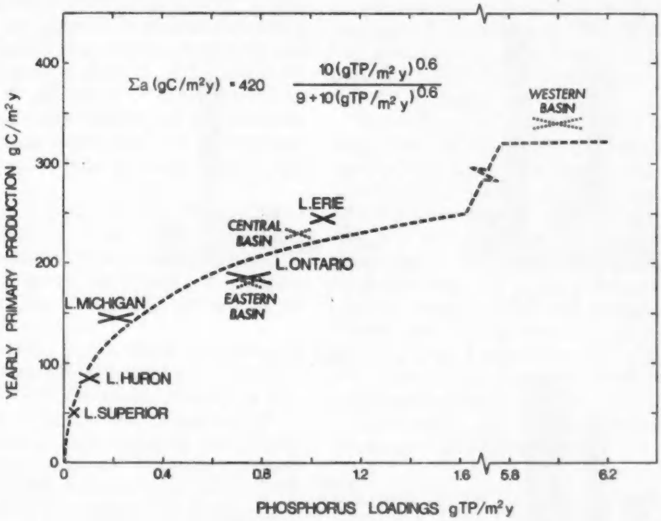


FIG. 11. Relation between annual primary production and annual phosphorus loading (Vollenweider).

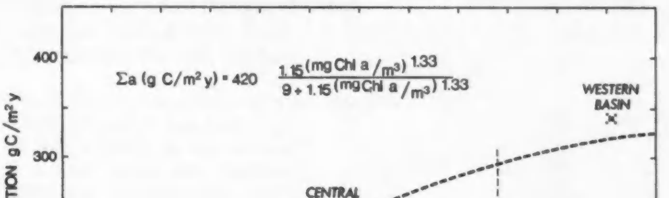


FIG. 12. Relation between annual primary production and surface chlorophyll *a* concentrations (Vollenweider).

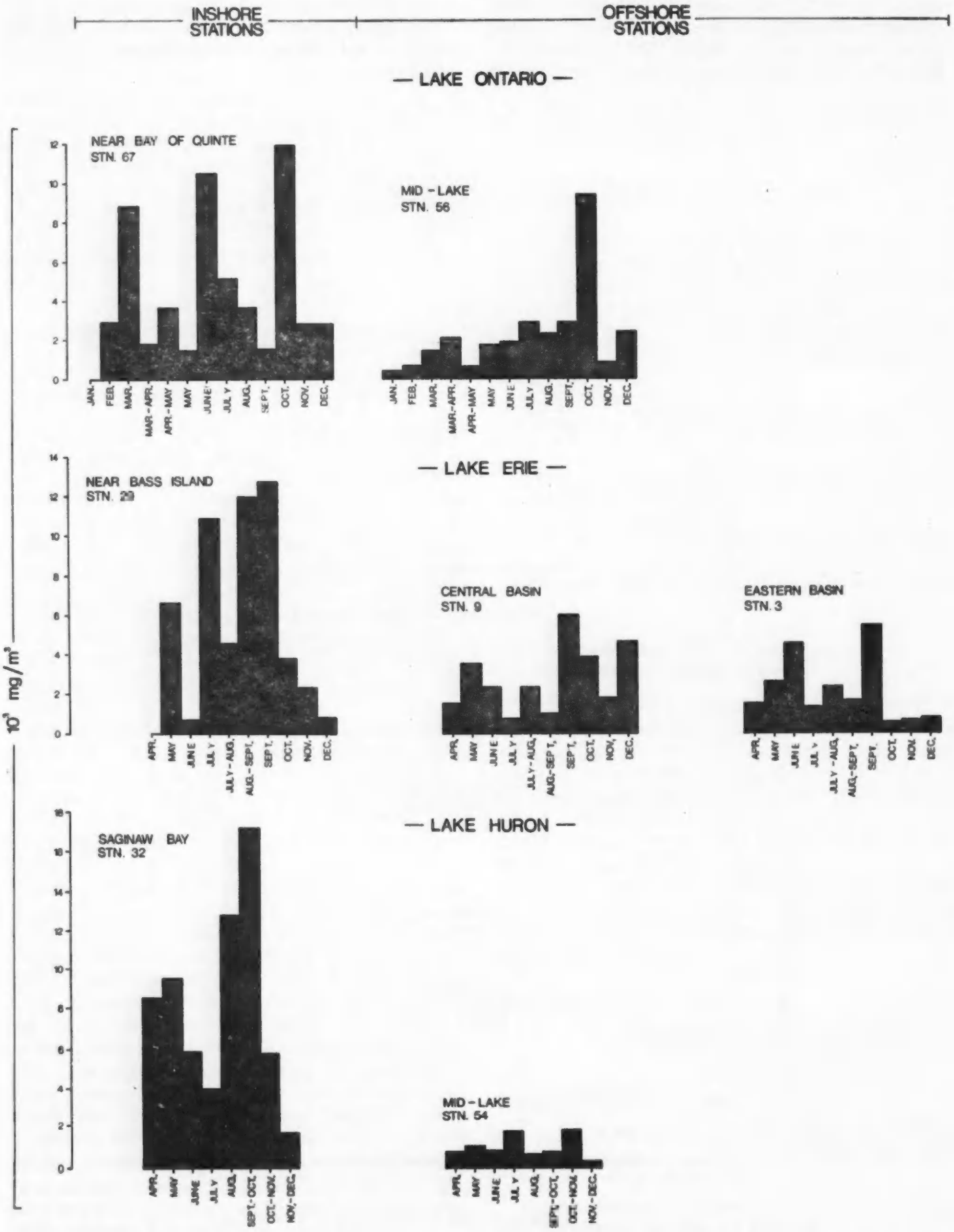


FIG. 13. Comparison of phytoplankton biomass at inshore and offshore stations of lakes Ontario, Erie, and Huron during 1970 and 1971 (M. Munawar and I. F. Munawar unpublished data).

TROPHIC CLASSIFICATION OF THE LAURENTIAN GREAT LAKES

The limitations and shortcomings of the classical trophic classification of lakes along the oligotrophic–eutrophic series is well known (Elster 1958; Rodhe 1958), and not yet solved (Vollenweider 1968). The terms oligotrophic, mesotrophic, and eutrophic are still used without a definite and universally acceptable scale of reference. The terminological problem has further been aggravated by confusion resulting from the increasing number of incidents of artificially eutrophied but basically oligotrophic lakes.

This problem is evident in the Great Lakes. Basically, these lakes, in their pristine stage, are oligo- to mesotrophic, but today they are eutrophied by man to various degrees. Accordingly, any trophic classification based on recent analyses reflects an artificial situation.

How far is it possible to rate the Great Lakes in terms of trophic status as projected from experience gained on other lakes? The main difficulty is that these large bodies of water cannot be treated as units without incurring inconsistencies. The breakdown into basins is possible for Lake Erie because of its general morphology; in the upper lakes a few bays can be identified as having properties different from the main body, but the greatest difficulty comes from the different regime "inshore–offshore," particularly evident in the case of Lake Ontario, and also of Lake Michigan. For these lakes, the question arises as to which of the regions should be selected to attach a trophic denomination to the lake as a whole. This question has not yet been answered.

An attempt to attach definite meanings to the terms "oligo-, meso, and eutrophy" has been made by Dobson et al. (in this volume) on the basis of average chlorophyll *a* and Secchi disc readings. Although this is not new (Vollenweider 1968), it is an attempt to overcome a certain subjectivity but as a whole remains intuitive.

The problem became evident when applied to our production estimates. In Fig. 11 the ranges defined by Dobson et al. on the basis of average chlorophyll has been reported and projected to annual primary production. Accordingly, oligotrophic lakes would have total annual production rates up to 100 g C/m^2 per yr, mesotrophic from 100 to 200 g C/m^2 per yr, and eutrophic $>$200 g C/m^2 per yr. In this scheme, the only eutrophic body of water would be the Western Basin of Lake Erie (also Saginaw Bay, for which we have no numeric estimate as yet).

However, other investigators, notably Vinberg (1961) and Rodhe (1969), have related their terminology to different ranges of annual production. Rodhe restricts his usage of the term "oligotroph" to lakes having an annual production up to 25 g C/m^2 per yr which is similar to the usage made by Vinberg (up to 30 g C/m^2 per yr). Lakes having an annual production of more than 300 g C/m^2 per yr are considered "polluted" by Rodhe and "highly eutrophic" by Vinberg. Both give a considerable range to what they call "mesotrophic," i.e. from 75 to 250 g C/m^2 per yr (Rodhe) and 30–200 g C/m^2 per yr (Vinberg).

Accordingly, all our lakes and basins, with the exception of Lake Superior on one end of the scale, and western Lake Erie on the other end, would be identified as mesotrophic in the above scheme, whereas Lake Huron would be in transition and Western Lake Erie would fall under the "highly eutrophic" or "polluted" classification. Though with this more general usage of terminology the ambiguities are not eliminated entirely, the scheme of Rodhe and Vinberg seems to be more appropriate for the Great Lakes than the simple breakdown into three categories only. Furthermore, it is also applicable to localized areas.

Accordingly, the following scheme summarizes the stage of the Great Lakes:

Trophic Scheme for the Laurentian Great Lakes

Oligotrophic	Mesotrophic	Secondary* eutrophic	Highly eutrophic polluted
Lake Superior			
Lake (offshore)	*Huron* (inshore)		Saginaw Bay
	Lake	*Erie*	
	Eastern Basin	Central Basin	Western Basin
	Lake	*Ontario*	
	(offshore)	(inshore)	(Bay of Quinte)
	Lake Michigan		
(offshore)		(inshore)	(Green Bay)

*"Secondary eutrophic" is used here in the sense of lake regions showing relatively high annual primary production, occurrence of occasional algal blooms, and/or increased growth of periphyton (cladophora) or macrophytes due to local pollution.

This scheme, based on annual production, agrees reasonably well with biomass data. In Fig. 13 the yearly variations of biomass of a few typical stations are reported. According to a scheme proposed by Vollenweider (1968) the maximum biomass attained during a year cycle would remain below 1 × 10^3 mg/m^3 in an ultraoligotrophic lake but would exceed 10 × 10^3 mg/m^3 in highly eutrophic lakes. Lakes of meso- to eutrophic character would show intermediate biomass densities. A more refined breakdown and a better definition of biomass ranges are under elaboration.

Acknowledgments

We thank Dr W. A. Glooschenko for providing manuscripts on primary production of lakes Ontario, Erie, and Huron (in press). They also express their appreciation to Dr N. Watson and Mr H. F. Nicholson, who made available Lake Superior data. The assistance of Mr J. E. Moore and Mrs I. F. Munawar in primary production and phytoplankton work is gratefully acknowldged.

AYERS, J. C., AND E. SEIBEL. 1973. Benton Harbor power plant limnological studies. Univ. Mich. Great Lakes Res. Div. Spec. Rep. 44: 57 p.

BRAIDECH, T. E., P. E. GEHRING, AND C. O. KLEVENO. 1971. Biological studies of oxygen depletion and nutrient regeneration processes in the Lake Erie Central Basin, p. 805–817. *In* Proc. 14th Conf. Great Lakes Res. 1971. Int. Assoc. Great Lakes Res.

BURKHOLDER, P. R. 1929a. Microplankton studies in Lake Erie. Bull. Buffalo Soc. Nat. Sci. 14: 73–93.

1929b. Microplankton studies in Lake Erie. New York Conserv. Dep. Annu. Rep. (Suppl.) 18: 60–66.

1960. A survey of the microplankton of Lake Erie. U.S. Fish. Wildl. Serv. Spec. Sci. Fish Rep. 334: 123–144.

CAPERON, J., AND J. MEYER. 1972. Nitrogen limited growth of marine phytoplankton. I. Changes in population characteristics with steady-state growth rate. Deep-Sea Res. 19: 601–618.

CASPER, V. L. 1965. A phytoplankton bloom in Western Lake Erie, p. 29–35. *In* Proc. 8th Conf. Great Lakes Res. Univ. Mich. Great Lakes Res. Div. Publ. 13.

CHANDLER, D. C. 1940. Limnological studies of Western Lake Erie. I. Plankton and certain physical chemical data of the Bass Islands region, from September 1938 to November 1939. Ohio J. Sci. 40: 291–336.

1942. Limnological studies of Western Lake Erie. III. Phytoplankton and physical-chemical data from November 1939 to November 1940. Ohio J. Sci. 42: 24–44.

1944. Limnological studies of Western Lake Erie. IV. Relation of limnological and climatic factors to phytoplankton of Western Lake Erie. Trans. Am. Microsc. Soc. 63: 203–236.

CLAFLIN, L. W., AND A. M. BEETON. 1972. Seasonal changes in the composition of phytoplankton of inshore Lake Michigan. Presented at 15th Conf. Great Lakes Res. Conf., Madison, Wis. (unpublished)

DALEY, R. J. 1971. Methodology and characterization of lacustrine chlorophyll diagenesis. Thesis. Queens Univ., Kingston, Ont.

DAVIS, C. C. 1954a. A preliminary study of the plankton of the Cleveland Harbour area, Ohio. II. The distribution and quantity of the phytoplankton. Ecol. Monogr. 24: 321–347.

1954b. A preliminary study of the plankton of the Cleveland Harbour area, Ohio. III. The zooplankton, and general ecological considerations of phytoplankton and zooplankton production. Ohio J. Sci. 54: 388–408.

1964. Evidence for the eutrophication of Lake Erie from phytoplankton records. Limnol. Oceanogr. 9: 275–283.

1965. The standing stock of phytoplankton in Lake Erie at Cleveland, Ohio, 1964. Inf. Bull. Planktol. Japan. 12: 51–53.

1966. Plankton studies in the Great Lakes of the world with special reference to the St. Lawrence Great Lakes of North America. Univ. Mich. Great Lakes Res. Div. Publ. 14: 54 p.

1969. Plants in Lakes Erie and Ontario and changes of their numbers and kinds, p. 18–44. *In* Proc. of Conf. on Changes in the Biota of Lakes Erie and Ontario. Bull. Buffalo Soc. Nat. Sci. 25.

DOBSON, H. F. H., M. GILBERTSON, AND P. G. SLY. 1974. A summary and comparison of nutrients and related water quality in lakes Erie, Ontario, Huron, and Superior. J. Fish. Res. Board Can. 31: 731–738.

ELSTER, H. J. 1958. Das limnologische Seetypensystem, Ruckblick und Ausblick. Verh. Int. Ver. Limnol. 13: 101–120.

EPPLEY, R. W. 1972. Temperature and phytoplankton growth in the sea. Fish. Bull. 70: 1063–1065.

FEE, E. J. 1971. A numerical model for the estimation of integral primary production and its application to Lake Michigan. Ph.D. Thesis Univ. Wis. 169 p.

FENWICK, M. G. 1962. Some interesting algae from Lake Huron. Trans. Am. Microsc. Soc. 81: 72–76.

1968. Lake Huron distribution of *Tabellaria fenestrata* var. *geniculata* A. Cleve and *Coelastrum reticulatum* var. *polychordon* Korshik. Trans. Am. Microsc. Soc. 87: 376–383.

GÄCHTER, R., R. A. VOLLENWEIDER, AND W. A. GLOOSCHENKO. 1974. Seasonal variations of temperature and nutrients in the surface waters of lakes Ontario and Erie. J. Fish. Res. Board Can. 31: 275–290.

GLOOSCHENKO, W. A., J. E. MOORE, M. MUNAWAR, AND R. A. VOLLENWEIDER. 1974a. Primary production in lakes Ontario and Erie: a comparative study. J. Fish. Res. Board Can. 31: 253–263.

GLOOSCHENKO, W. A., J. E. MOORE, AND R. A. VOLLENWEIDER. 1972. The seasonal cycle of pheopigments in Lake Ontario with particular emphasis on the role of zooplankton grazing. Limnol. Oceanogr. 17: 597–605.

1973. Chlorophyll *a* distribution in Lake Huron and its relationship to primary production. *In* Proc. 16th Conf. Great Lakes Res., Int. Assoc. Great Lakes Res. (In press)

1974b. Spatial and temporal distribution of chlorophyll *a* and pheopigments in surface waters of Lake Erie. J. Fish. Res. Board Can. 31: 265–274.

Gottschall, R. Y. 1930. Preliminary report on the phytoplankton and pollution in Presque Isle Bay, Lake Erie. Proc. Pennsylvania Acad. Sci. 4: 69–70.

Gottschall, R. Y., and O. E. Jennings. 1933. Limnological studies at Erie, Pa. Trans. Am. Microsc. Soc. 52: 181–191.

Harris, G. P. 1973. The diel and annual cycles of net plankton photosynthesis in Lake Ontario. J. Fish. Res. Board Can. 30: 1779–1787.

Harris, G. P., and J. N. A. Lott. 1973a. Light intensity and photosynthetic rates in phytoplankton. J. Fish. Res. Board Can. 30: 1771–1778.

1973b. Observations of Langmuir circulations in Lake Ontario. Limnol. Oceanogr. 18: 584–589.

Hohn, M. H. 1969. Qualitative and quantitative analyses of plankton diatoms, Bass Island area, Lake Erie, 1938–1965, including synoptic surveys of 1960–1963. Ohio State Univ. Bull. Ohio Biol. Surv. New 3: 211.

Holland, R. E. 1968. Correlation of *Melosira* spp. with trophic conditions in Lake Michigan. Limnol. Oceanogr. 13: 555–557.

1969. Seasonal fluctuations of Lake Michigan diatoms. Limnol. Oceanogr. 14: 423–436.

Holland, R. E., and A. M. Beeton. 1972. Significance to eutrophication of spatial differences in nutrients and diatoms in Lake Michigan. Limnol. Oceanogr. 17: 88–96.

Holm-Hansen, O. 1969. Determination of biomass in ocean profiles. Limnol. Oceanogr. 14: 740–747.

1972. Total microbial biomas estimation by the ATP method. *In* Y. I. Sorokin and H. Kadota [ed.] Microbial production and decomposition in fresh waters. IBP Handbook No. 23, Blackwell Scientific Publ., Oxford. p. 71–76.

IJC. 1969. Report to the International Joint Commission on the pollution of Lake Erie, Lake Ontario and the international section of the St. Lawrence River. 000 p.

1973. Great Lakes Water Quality Annual Report to the International Joint Commission. Great Lakes Water Quality Board, Apr., 1973. 315 p.

Kellicott, D. S. 1878. Notes on microscopic life in the Buffalo water supply. Am. J. Microsc. Pop. Sci. 3: 250–252.

Kramer, J. R., H. E. Allen, G. H. Baulne, and N. M. Burns. 1970. Lake Erie Time Study (LETS). Can. Cent. Inland Waters Pap. 4: 14 p.

Lee, G. F. 1974. Phosphorus, water quality and eutrophication of Lake Michigan. Presented at Lake Mich. Enforcement Conf. 1972. (unpublished)

Megard, R. O. 1972. Phytoplankton, photosynthesis and phosphorus in Lake Minnetonka, Minnesota. Limnol. Oceanogr. 17: 68–87.

Mills, H. 1882. Microscopic organisms in the Buffalo water supply and in Niagara River. Proc. Am. Soc. Microsc. 5: 165–175.

Munawar, M. 1973. Comparative studies upon the phytoplankton of the Great Lakes with emphasis on phytoflagellates. Presented at Symp. on Freshwater Algology, Can. Bot. Assoc. Univ. Western Ont., London, Ont. (unpublished)

Munawar, M., and A. Nauwerck. 1971. The composition and horizontal distribution of phytoplankton in Lake Ontario during the year 1970, p. 69–78. *In* Proc. 14th Conf. Great Lakes Res., Int. Assoc. Great Lakes Res.

Nalewajko, C. 1966. Composition of phytoplankton in surface waters of Lake Ontario. J. Fish. Res. Board Can. 23: 1715–1725.

1967. Phytoplankton distribution in Lake Ontario Proc. 10th Conf. Great Lakes Res., Int. Assoc. Great Lakes Res. p. 63–69.

Nauwerck, A. 1963. The relation between zooplankton and phytoplankton in Lake Erken. Symb. Bot. Uppsal. (Upps.) 17(5): 163. (In German)

Olive, J. H., D. M. Benton, and J. Kishler. 1969. Distribution of C-14 in products of photosynthesis and its relationship to phytoplankton composition and rate of photosynthesis. Ecology 50(3): 380–386.

Olson, T. A., and T. O. Odlaug. 1966. Limnological observation on Western Lake Superior. Univ. Mich. Great Lakes Res. Div. Publ. 15: 109–118.

Parkos, W. G., T. A. Olson, and T. O. Odlaug. 1969. Water quality studies on the Great Lakes based on C-14 measurements on primary productivity. Univ. Minn., Water Resour. Res. Cent. Bull. 17: 121 p.

Parsons, T. R., K. Stephens, and J. D. H. Strickland. 1961. On the chemical composition of eleven species of marine phytoplanketers. J. Fish. Res. Board Can. 18: 1001–1016.

Patalas, K. 1972. Crustacean plankton and the eutrophication of St. Laurentian Great Lakes. J. Fish. Res. Board Can. 29: 1451–1462.

Putnam, H. D., and T. A. Olson. 1961. Studies on the productivity and plankton of Lake Superior. Univ. Rep. Sch. Public Health. Minn. 24 p.

1966. Primary productivity at a fixed station in Western Lake Superior, p. 115–128. *In* Proc. 9th Conf. Great Lakes Res., Int. Assoc. Great Lakes Res.

Robertson, A., C. F. Powers, and J. Rose. 1971. Distribution of chlorophyll and its relation to particulate organic matter in the offshore waters of Lake Michigan, p. 90–101. *In* Proc. 14th Conf. Great Lakes Res., Int. Assoc. Great Lakes Res.

Rodhe, W. 1958. Primarproduktion und Seetypen. Verh. Int. Ver. Limnol. 13: 121–141.

1969. Crystallization of eutrophication concepts in Northern Europe, p. 50–64. *In* Eutrophication: causes, consequences, correctives. Nat. Acad. Sci., Washington, D.C.

SAUNDERS, G. W. 1964. Studies of primary productivity in the Great Lakes. Univ. Mich. Great Lakes Res. Div. Publ. 11: 122–129.

SAUNDERS, G. W., F. B. TRAMA, AND R. W. BACHMAN. 1962. Evaluation of a modified C-14 technique for shipboard estimation of photosynthesis in large lakes. Univ. Mich. Great Lakes Res. Div. Publ. 8: 61 p.

SCHELSKE, C. L., AND E. CALLENDER. 1970. Survey of phytoplankton productivity and nutrients in Lake Michigan and Lake Superior, p. 93–105. *In* Proc. 13th Conf. Great Lakes Res., Int. Assoc. Great Lakes Res.

SCHELSKE, C. L., L. E. FELDT., M. A. SANTIAGO, AND E. F. STOERMER. 1972. Nutrient enrichment and its effect on phytoplankton production and species composition in Lake Superior, p. 149–165. *In* Proc. 15th Conf. Great Lakes Res., Int. Assoc. Great Lakes Res.

SCHELSKE, C. L., AND J. C. ROTH. 1973. Limnological survey of lakes Michigan, Superior, Huron and Erie. Univ. Mich., Great Lakes Res. Div. Publ. 17: 108 p.

SCHELSKE, C. L., E. F. STOERMER, AND L. E. FELDT. 1971. Nutrients, phytoplankton productivity, and species composition as influenced by upwelling in Lake Michigan, p. 102–113. *In* Proc. 14th Conf. Great Lakes Res., Int. Assoc. Great Lakes Res.

STADELMANN, P., J. E. MOORE, AND E. PICKETT. 1974. Primary production in relation to temperature structure, light condition and biomass at an inshore and offshore station in Lake Ontario. J. Fish. Res. Board Can. 31.

STOERMER, E. F., C. L. SCHELSKE, AND L. E. FELDT. 1971. Phytoplankton assemblage differences at inshore versus offshore stations in Lake Michigan and their effects on nutrient enrichment experiments, p. 114–118. *In* Proc. 14th Conf. Great Lakes Res., Int. Assoc. Great Lakes Res.

STOERMER, E. F., C. L. SCHELSKE, M. A. SANTIAGO, AND E. F. FELDT. 1972. Spring phytoplankton abundance and productivity in Grand Traverse Bay, Lake Michigan, 1970: 15th Conf. Great Lakes Res. p. 181–191.

STOERMER, E. F., AND J. J. YANG. 1970. Plankton Assembly in Lake Michigan. Univ. Mich. Great Lakes Res. Div. Spec. Rep. 47: 268 p.

STRICKLAND, J. D. H. 1960. Measuring the primary production of marine phytoplankton. Bull. Fish. Res. Board Can. 122.

TAFT, C. E., AND C. W. TAFT. 1971. The algae of Western Lake Erie. Ohio State Univ. Bull. Ohio Biol. Surv. New Ser. 4. 189.

TIFFANY, L. H. 1934. The plankton algae of the west end of Lake Erie. Contrib. F. T. Stone Lab. 6: 112 p.

UTERMÖHL, H. 1958. Zur Vervolkommung der quantitätiven Phytoplankton. Method. Mitt. Int. Verein. Limnol. 9: 1–38.

VERDUIN, J. 1951. Comparison of spring diatom crops of Western Lake Erie in 1949 and 1950. Ecology 32: 662–668.

1952. Photosynthesis and growth rates of two diatom communities in Western Lake Erie. Ecology 33: 163–168.

1960. Phytoplankton communities of Western Lake Erie and the CO_2 and O_2 changes associated with them. Limnol. Oceanogr. 5: 372–380.

1964. Changes in Western Lake Erie during the period 1948–1962. Verh. Int. Verein. Limnol. 15: 639–644.

1972. Metabolism of the dominant autotrophs of the North American Great Lakes. Verh. Int. Verein. Limnol. 18: 105–112.

VINBERG, G. G. 1961. Modern conditions and problems in the study of primary production of waters. Referat. Zhur. Biol. Minsk. (1962) 22Zh329: 11–24.

VOLLENWEIDER, R. A. 1960. Beitrage zur Kenntnis optischer Eigenschaften und Primärproduktion. Mem. Ist. Ital. Idrobiol. Dott Marco de March Pallanza, Italy. 12: 201–244.

1965. Calculation models of photosynthesis-depth curves and some implications regarding day rate estimates in primary production measurements. Proc. IBP Symp. Primary Productivity in Aquatic Environments, Pallanza, Italy. Mem. Ist. Ital. Idrobiol. Dott Marco de Marchi Pallanza, Italy. 18: 425–457.

1968. Scientific fundamentals of the eutrophication of lakes and flowing waters, with particular reference to nitrogen and phosphorus as factors in eutrophication. Organ. Econ. Coop. Dev. (Paris) Tech. Rep. DAS/CSI/68.27. p. 182.

1970. Models for calculating integral photosynthesis and some implications regarding structural properties of the community metabolism of aquatic systems. Proc. IBP/PP Tech. Meet. Trebon. Cent. Agric. Publ. Doc., Wageningen, Netherlands p. 455–472.

WRIGHT, S., L. H. TIFFANY, AND W. M. TIDD. 1955. Limnological survey of Western Lake Erie. U.S. Fish. Wildl. Serv. Spec. Sci. Fish Rep. 139–1–341.

WUJEK, D. E. 1967. Some plankton diatoms from the Detroit River and the Western end of Lake Erie adjacent to Detroit River. Ohio J. Sci. 67: 32–35.

Benthic Macroinvertebrates of the St. Lawrence Great Lakes[1]

DAVID G. COOK AND MURRAY G. JOHNSON

Department of the Environment, Fisheries and Marine Service
Great Lakes Biolimnology Laboratory
Canada Centre for Inland Waters, Burlington, Ont. L47 4A6

COOK, D. G., AND M. G. JOHNSON. 1974. Benthic macroinvertebrates of the St. Lawrence Great Lakes. J. Fish. Res. Board Can. 31: 763–782.

The history of Great Lakes benthic research from 1870 to the present is briefly reviewed. An examination of the status of taxonomic work on benthic components, and a consideration of the zoogeographical history of the benthos leads to a discussion of bottom communities and macroinvertebrate production in the five major lakes.

Profundal communities throughout the lakes are dominated by the glaciomarine relict amphipod *Pontoporeia affinis* and various species of Oligochaeta, Sphaeriidae, and Chironomidae. The specific composition of these components, and natural and recently imposed changes in their proportions within communities are examined. Population densities and standing stocks, and the proportion of oligochaetes in communities, all tend to increase in response to a natural gradient in productivity inferred from increasing concentrations of parameters such as organic matter and water hardness. Man's influence on water quality anywhere along this gradient compounds the effects of natural factors towards tubificid communities of predictable species composition: *Limnodrilus hoffmeisteri*, *L. claparedeianus*, *L. cervix*, *L. maumeensis*, *Peloscolex multisetosus*, and often *Tubifex tubifex*. The ameliorating influence of water depth is shown in Lake Erie where the change in community composition reflects improving profundal water quality from west to east — a reversed model of the Great Lakes system as a whole.

COOK, D. G., AND M. G. JOHNSON. 1974. Benthic macroinvertebrates of the St. Lawrence Great Lakes. J. Fish. Res. Board Can. 31: 763–782.

Nous faisons un bref historique des recherches benthiques effectuées dans les Grands lacs de 1870 à nos jours. L'examen de l'état des travaux taxonomiques sur la composition du benthos et son histoire zoogéographique débouche sur une analyse des communautés benthiques et de la production des macroinvertébrés dans les cinq lacs principaux.

L'amphipode glacio-marin relictuel *Pontoporeia affinis* et diverses espèces d'Oligochaeta, Sphaeriidae et Chironomidae dominent dans les communautés des profondeurs à la grandeur des lacs. Nous examinons la composition spécifique de ces constituants, de même que les changements naturels récents imposés à leurs proportions au sein de la communauté. La densité et la biomasse des populations, ainsi que la proportion des oligochètes dans les communautés ont toutes tendance à augmenter en réponse à un gradient naturel de productivité, gradient qui se reflète dans des concentrations croissantes de variables telles que matière organique et dureté de l'eau. L'influence de l'homme sur la qualité de l'eau, à n'importe quel point de ce gradient, s'ajoute aux facteurs naturels pour produire des communautés de tubificides de composition spécifique prévisible: *Limnodrilis hoffmeisteri*, *L. claparedeianus*, *L. cervix*, *L. maumeensis*, *Peloscolex multisetosus*, et souvent *Tubifex tubifex*. L'influence salutaire de la profondeur de l'eau apparaît dans le lac Erié, où le changement dans la composition de la communauté reflète une eau profonde dont la qualité s'améliore de l'ouest à l'est — un modèle inverse du régime des Grands lacs dans leur totalité.

Accepted December 31, 1973

HISTORICAL aspects of benthic investigations of the Great Lakes and the motives which stimulated them have been succinctly summarized by Henson (1966) for the period from 1870 to the early 1960's. The earliest and very brief records of Great Lakes benthos, taken for reasons of academic curiosity, came from inshore waters of Lake Superior (Jackson 1844; Agassiz 1850), whereas the studies of Stimpson (1871) and Hoy (1872) on Lake Michigan, and Smith and Verrill (1871) and Smith (1874b) on Lake Superior, concerned deeper waters

---

[1] This paper, part of a special issue that comprises a comprehensive review of Limnology in Canada, was prepared to mark the 19th Congress of the International Association of Limnology (SIL), in Winnipeg, Man., during August 1974.

Printed in Canada (J3260)

and were initiated primarily to discover the nature of the food resources supporting the fish populations. Nicholson (1873) adopted a more academic approach in his survey of Lake Ontario near Toronto, but thereafter benthic studies were usually associated with fisheries problems (Reighard 1894; Ward 1896; Adamstone 1924; Eggleton 1936, 1937; Shelford and Boesel 1942) or pollution impact and assessment work (Brown 1953; Alley and Powers 1970) or both (Wright and Tidd 1933; Wright 1955). Benthological studies postdating Henson's (1966) review include the work of Schuytema and Powers (1966), Brinkhurst (1967, 1969, 1970), Brinkhurst et al. (1968), Hiltunen (1967, 1969a, 1969b, 1969c), Johnson and Matheson (1968), Powers and Robertson (1968), Veal and Osmond (1968), Adams and Kregear (1969), Howmiller and Beeton (1970, 1971), Johnson and Brinkhurst (1971a, 1971b, 1971c), and Mozley and Garcia (1972).

The drastic decline in commercial fisheries in the 1940s and 1950s with the growing awareness of technological man's deleterious impact on his environment in the 1950s and 1960s culminating in public involvement in biological affairs, resulted in, and continues to produce, large bodies of benthological data. However, the value of some of this work is questionable because investigators were unable, (through gaps in knowledge) or unwilling to identify their material to the basic biological unit — the species; it would seem that to attempt an investigation of any biological system without defining species precisely is as fruitless as studying a chemical reaction without knowledge of the elements. Thus it is pertinent to review briefly the various major components of Great Lakes benthos and to indicate the status of their taxonomy. Subsequent sections will attempt to explain the origins of benthic fauna, and will consider the distribution and abundance of various components in the five major lakes. A synthetic descriptive treatment of the whole Great Lakes system is then attempted, with observations on benthic productivity and comparisons with Palaearctic lakes.

Taxonomy of Benthic Components

For the purposes of this systematic overview, the lakes may be visualized as being composed of two major habitats: the profundal zone is a large region of rigorous but, with the exception of oxygen concentrations, comparatively uniform environmental conditions, inhabited by a few very abundant species; the spatially limited but ecologically important shallow water or inshore zone, however, is characterized by highly variable physical conditions and high species diversity.

The major macroscopic components of the profundal benthos belong to only four major taxa, three of which (Oligochaeta, Chironomidae, and Sphaeriidae) have been summarized in Brinkhurst et al. (1968); in terms of abundance and biomass, amphipod crustaceans dominate clean benthic environments, and fortunately their taxonomy is well documented (Bousfield 1958; Holsinger 1972) and distribution is known in some detail; *Pontoporeia affinis* is the dominant, and often the only, profundal amphipod and may reach abundances of 14,000 per square meter (reviewed in Henson 1966, 1970). In the Oligochaeta, the lumbriculid *Stylodrilus heringianus* occurs in significant numbers over much of the upper lakes and deep basins of the lower lakes, and the Tubificidae assume a major role, especially in the lower lakes and enriched habitats of Superior, Michigan, and Huron. The taxonomy of tubificids was chaotic until the 1960s, and benthologists usually identified to the familial or generic level only; but the studies of Brinkhurst (1963, 1965) and Brinkhurst et al. (1968, 1971) provided workable keys to the group and thereby stimulated some valuable contributions to lake biology (eg. Hiltunen 1967, 1969a; Brinkhurst 1967). Some taxonomic problems do remain, however; for example, *Limnodrilus* species are distinguished mainly by the shape and dimensions of their highly developed penes, and some populations have been examined (D. G. Cook unpublished data) which consist of normal *L. hoffmeisteri* (a very tolerant animal, large numbers of which have been associated with organic pollution — Brinkhurst 1967; Brinkhurst et al. 1971) *L. claparedeianus* (probably equally tolerant), and an entity variously referred to as *L. spiralis* (?) (Hiltunen 1969a) or *L. hoffmeisteri*, 'variant' (Brinkhurst et al. 1971); a preliminary analysis of the available data suggests that the latter is in fact an interspecific hybrid of *L. claparedeianus* and *L. hoffmeisteri*. *L. claparedeianus* and *L. cervix* have also been recorded as having 'typical' or 'atypical' penes (Hiltunen 1967, 1969a).

A group of small bivalves, the Sphaeriidae (fingernail or pea clams), occur ubiquitously in the Great Lakes, and despite the sound systematic studies of Herrington (1962) and Burch (1972) they continue to frustrate benthic biologists because of their high degree of variability and fine taxonomic distinctions.

The Chironomidae (Insecta, Diptera), which occur throughout the lakes, are also a difficult group. The work of Hamilton et al. (1969) has done much to stabilize their confused nomenclature; Mason (1968) contributed an illustrated key to common genera, and Sæther (1969, 1973) provided descriptions or keys to species for a number of important genera. However, chironomids will continue to be troublesome until more life-history studies have been completed. The predatory Chaoboridea (Diptera), which perform daily vertical migrations (Jónasson 1972), have also been treated by Sæther (1970).

Despite relative ease of access to inshore areas of the Great Lakes, the distribution, ecology, and taxonomy of the shallow water benthos is generally poorly known: basically it differs from the profundal fauna by the larger number of species occurring in relatively low numbers in the great range of microhabitats provided by physical conditions of the littoral zone, and its diverse macroflora. The inshore fauna is composed of a number of species in the major profundal groups Chironomidae, Sphaeriidae, Oligochaeta (especially Naididae), and Amphipoda (*Gammarus*), and of representatives of the following taxa which are sensitive to depth related factors, or which are competitively excluded from the profundal environment. In terms of biomass, the molluscs dominate shallow waters. Except for the overdescribed *Anodonta* species (LaRocque 1967), the filter-feeding Pelecypoda (bivalves, clams) present no great taxonomic difficulty at the species level (Goodrich and van der Schalie 1932; Clark and Berg 1959; Heard and Burch 1966), but many herbivorous gastropod families (snails) are in need of systematic revision. Despite Goodrich's (1932) and LaRocque's (1953) summaries of exisiting taxonomic information on the snails of Michigan and Canada, respectively, the Planorbidae, Physidae, Pleuroceridae, Lymnaeidae, and Valvatidae all contain problematical or dubious entities; the Amnicolidae are better known (Berry 1943). Clarke (1973) has provided excellent summaries of snails and clams found in the Canadian interior basin, many of which originated from Great Lakes populations.

Many groups of insects inhabit the littoral zone of lakes, and, like chironomids, are generally in need of taxonomic review or life history studies to correlate adult and juvenile forms. This is true of the two most important orders, Ephemeroptera and Trichoptera, except for the most common species or those which have largely disappeared from their natural habitats due to cultural eutrophication (e.g. Britt's work (1955) on *Hexagenia* in western Lake Erie). Some areas are better known, however, due to the activities of a few specialists; examples are the Ephemeroptera of Georgian Bay, Lake Huron, which were studied by Clemens (1915), and the adult Trichoptera of western Lake Erie reviewed by Marshall (1939). Other groups which inhabit mainly the littoral zone in nymphal or larval condition include Odonata, Plecoptera, Neuroptera, Lepidoptera, and many dipteran families, and adults and juvenile Hemiptera and Coleoptera are also found; many of these groups swim actively and can be considered as truely benthic only part of the time.

Crustacea other than amphipods which perform a significant role in littoral and sublittoral habitats are the conspicuous and well-documented Decapoda (Crocker and Barr 1968) and the less thoroughly known Isopoda (Williams 1970). The mainly predatory Hirudinea have recently been reviewed, and workable keys have been provided by Davies (1971) and Sawyer (1972). The Turbellaria (flatworms) can be identified (Kenk 1972) but often require tedious manipulation. Gannon (1972) has summarized our knowledge of the Acari (mites) for Lake Michigan, with some data on lakes Huron and Erie.

Minor components of both profundal and inshore benthos, or components which occur sporadically, are often of great taxonomic difficulty; North American nematodes and Enchytraeidae (Oligochaeta) are virtually unknown, but both may be found occasionally in large numbers. The microscopic and interstitial benthos, including a number of aschelminths, tardigrades, protozoa, and Aeolosomatidae (Annelida), are suspected to fill an important energy level in the trophic structure of the benthos but are often tedious to work with or are difficult or unknown taxonomically.

Unless otherwise stated, the nomenclature used in this account is consistent with the following works: Amphipoda, Bousfield 1958; Decapoda, Crocker and Barr 1968; Oligochaeta, Brinkhurst and Jamieson 1971; Sphaeriidae, Herrington 1962; Chironomidae, Hamilton et al. 1969.

Thus, although much has been accomplished since Henson's (1966) review, especially in oligochaete and chironomid systematics, the observation that "a fundamental species inventory is needed as a foundation and basis to solve current problems" (p. 41) is still, regrettably, pertinent.

Zoogeography

The distribution of major faunal elements in the Great Lakes is remarkably uniform, considering the vast (246,600 square kilometers) area of the system. Generally, but with some notable exceptions, the lakes differ from each other quantitatively, not qualitatively; that is in abundance, not kind, of animals inhabiting the benthic environment. To understand the lakes as a whole biological system, it is therefore necessary to examine the following major questions. How did its benthic fauna originate? What factors control present distribution and abundance of its component species? How do these species interact to produce a balanced subsystem? How does the benthos interact with other biotic subsystems? Of the last three questions it is also of great importance to ask, how is the situation changing?

The first question is partly answerable by examining the geological history of the area and the distribution mechanisms available to potential components. Little is known about preglacial drainage patterns except that the present basins were probably occupied by a system of river valleys draining eastward, which were repeatedly deepened by successive glacial scouring and depression by the great mass of the ice sheet. When the last Wisconsin glacier began to retreat into the present Great Lakes basin about 14–15,000 years ago, meltwater became trapped between the high ground to the south and the ice sheet to the north, forming large glacial lakes whose pattern and drainage fluctuated with the minor advances and retreats of the last deglaciation. Pertinent details of this history (summarized in Hough 1962; Flint 1971) include the facts that precursors of the Great Lakes drained southwards into the Mississippi system a number of times throughout their formation, and that the upper lakes discharged through the Ottawa valley after the Valders maximum ice cover and were therefore isolated from the early lower lakes for a period, until the final ice retreat when the St. Lawrence lowlands and probably Lake Ontario were flooded by the St. Lawrence Sea.

The faunal colonization of this very young system (it stabilized only between 5–8000 years ago) probably began in the earliest ice-dammed lakes from two major sources — through the agency of the ice sheet and its associated phenomena as a means of transport, and through the active or passive dispersal of animals from the south in the wake of the retreating glacier.

It is contended by Ricker (1959) and Segerstråle (1962) that the ice sheet in its southward advance trapped and transported arctic marine or brackish water animals with the ice front, some of which survived and adapted to freshwater conditions of proglacial lakes; after the ice retreated, these so-called glaciomarine relicts became trapped in lake basins at the southern limit of the ice. Segerstråle (1962), however, further believes that relict species originated from the White Sea stock trapped in the Onega ice lake, and that initial dispersal occurred through the proglacial lakes to the Baltic basin and thence eastward through Siberia to the arctic coast of Canada in the penultimate (Illinoian) glaciation; the problem of land bridges, implied by Segerstråle's theories, is discussed in Frey (1965). Despite these differences concerning exact places of origin, a present-day distribution pattern, which more or less coincides with the southern limit of final glaciation, can be taken as good evidence that an animal is either a relict species or that it became dispersed exclusively through the glacial lake system; supplementary taxonomic evidence of intergeneric relations such as the existence or not of close marine forms usually decides this question. The important amphipod *Pontoporeia affinis* and the semi-planktonic *Mysis relicta* are considered to be true glaciomarine relicts, whereas the dominant profundal chironomid *Heterotrissocladius subpilosus* and the sphaeriid *Pisidium conventus* are similarly distributed (Henson 1966) cold-water animals having long freshwater lineages, and therefore are thought to have become dispersed through the proglacial lakes. An interesting explanation for the dominance of phylogenetically ancient crustaceans, which only recently left the sea, in the profundal regions of cold-water bodies, was suggested by Bousfield who believes that the more highly specialized crustacea evolved mainly in warm water and "have not yet solved the physiological problems of existing in harsh environments...and are thus unable to replace the ancient forms through direct competition" (quoted in Frey 1965, p. 626).

Segerstråle's (1962) belief in an all-freshwater route into North America from the Old World seems to be supported by the facts that *H. subpilosus* and *P. conventus* occur with *Mysis* and *Pontoporeia* in some north European lakes, and that other benthic elements whose dispersal occurs exclusively in freshwater are common to both regions. For example, most Naididae are holarctic animals, and of the 31 species of Tubificidae known to live in the Great Lakes (Brinkhurst et al. 1968) 19 are found also in Europe; it is possible that these oligochaetes, along with some other chironomids and sphaeriids, arrived in North America during or before the penultimate (Illinoian) glacial period and achieved their present distribution through the proglacial lakes and their associated fluctuating drainage patterns.

Brinkhurst (Brinkhurst et al. 1968), however, suggested that many oligochaetes may have been introduced into the Great Lakes and cites as examples of the tubificids *Peloscolex ferox*, some or all *Potamothrix* species, and the important profundal lumbriculid *Stylodrilus heringianus*. The facts that other members of *Stylodrilus* were unknown in North America, and that it seems unlikely that early workers on Great Lakes oligochaetes (Smith and Verrill 1871; Smith 1919) overlooked the distinct non-retractable penes of *S. heringianus*, strongly suggested recent introduction; however, indigenous species of *Stylodrilus* have now been discovered in two nonglaciated parts of the continent (a troglobiotic species in West Virginia and an epigean species in northwestern Yukon Territory, which was part of, or adjacent to, the Beringian glacial refugium — D. G. Cook in preparation); the latter, together with the fact that *S. heringianus* is distributed more widely than was previously thought (stream in Amherst, Massachusetts; Miramichi River, New Brunswick (unpublished data); "Manitoba" (Brinkhurst and Jamieson 1971, p. 110); Great Lakes basin) suggests pleistocene dispersal. The littoral lumbriculid *Eclipidrilus lacustris* from Lake Superior is certainly indigenous to North America and probably originated from Mississippi drainage populations; recently discovered Beringian refugium species of a genus probably derived from *Eclipidrilus* (or vice versa) seem to preclude the possibility of immigration from the North via Lake Nipigon.

Because of their conspicuous, easily preserved shells and great intrinsic beauty, the living and fossil molluscs have received considerable attention from amateur and professional naturalists for many years. Thus, their distribution is known in some detail and their historical zoogeography understood better than that of most invertebrates (Goodrich 1932; Goodrich and van der Schalie 1932; LaRocque 1953, 1967; Clarke and Berg 1959; Taylor 1965; Clarke 1969, 1973). Distribution patterns indicate that the rich pelecypod fauna of inshore Lake Erie was derived from Mississippi drainage stock (eg. *Truncilla donaciformis*, *Quadrula quadrula*) entering through the Maumee River which existed from about 15,000 to 13,500 years ago. The relatively restricted faunas of Lake Ontario and most of the upper lakes contain both Mississippian elements (e.g. *Proptera alata*, *Anodonta grandis*) and a few species originating from Atlantic seaboard populations (e.g. *Lampsilis radiata radiata*, *Anodonta implicata*, *Ligumia nasuta*) which gained access to Ontario through the Mohawk and Hudson valleys and later the St. Lawrence, and to the upper lakes through the Ottawa Valley.

Migration into, and dispersal within, the lakes was probably effected by the peculiar glochidium stage in the Unionid life cycle; these newly hatched individuals resemble miniature clams but are obligate parasites on the gills, fins, and general body surface of fish for 10–30 days before they detach to become free-living juveniles. Thus the restricted distribution of many clams to particular watershed or drainage systems is determined partly by the migrations of their fish hosts. The wide distribution exhibited by many species of the small, light, ovoviviparous, hermaphroditic, facultatively self-fertilizing Sphaeriidae is easily understood: they can be dispersed by wind, they have been observed attached to the legs of powerfully flying *Dytiscus* beetles (Kew 1888), and it was suggested by Heard (1962) that viable psidia can be transported through the digestive system of fish.

The two major entrance routes into the Great Lakes, as described for the pelecypods, were undoubtedly used by gastropods, decapod crustaceans, and other inshore groups; the extent to which they have colonized the lakes depends only on suitability and availability of living space, and on efficiency of their dispersal mechanisms. The former will be discussed in a subsequent section and examples of the latter have already been mentioned; however, in a number of freshwater animals, perhaps the most widely developed adaptive character which has arisen to ensure survival in a (geologically speaking) ephemeral habitat, is the ability to resist dessication at some stage in their life cycle; this strategy also enables small animals and eggs to be dispersed over a wide area by wind action and by various "ducks' feet" methods. The dispersal potential of such resistant phases is illustrated by an experiment quoted in Hesse et al. (1951, p. 421) in which water was added to dried mud from the flood area of the lower River Danube: living animals which emerged included *Apus* (Branchiopoda), Cladocera, Ostracoda, Tardigrada, a nematode, and several annelids and platyhelminths. Specialized dispersal mechanisms include that of many leeches whose ectoparasitic habit enables them to be transported overland to different drainage areas by birds and mammals; likewise, most insects have a winged adult stage and are therefore capable of colonizing new areas independent of regional hydrography.

Considering the extreme youth of the system, it may seem surprising that endemic speciation must also be discussed as a factor in the origin of Great Lakes benthos. However, organisms living under the harsh and variable conditions of the inshore zone are subject to intense selection pressures; therefore, relatively rapid genetic changes may occur which, cumulatively, result in speciation if a barrier to gene flow in and out of the population exists. The northern shore of Lake Superior is subject to continuous wave action which effectively isolates some littoral populations and Clarke (1969) has characterized the area as "the most active recent site for freshwater gastropod evolution in boreal eastern North America." In gastropods the evolutionary process has reached a state where distinct subspecies can be recognized, and Clarke (1969) lists seven of these (belonging to the genera *Valvata*, *Helisoma*, and *Lymnaea*) as unique to Lake Superior and adjacent regions of the Hudson Bay watershed.

The historical zoogeography of Great Lakes benthos may best be summarized by quoting Henson's (1966) view: "The littoral communities are dominated by a pre-Pleistocene native fauna that... migrated into the lake basins as the ice receded or was established in proglacial lakes. The profundal fauna is characterized by those species that inhabited the marginal proglacial lakes and during the Pleistocene migrated into the Great Lakes by routes determined by ice fronts." To this essentially dual origin it is necessary to add that in comparatively recent years man has characteristically complicated historic patterns by introducing foreign species into the Great Lakes (e.g. *Viviparus malleatus*, a Japanese gastropod; and *Bithinia tentaculata*, a north European snail imported in the late 1870s) or by opening up new freshwater connections between the lakes (Welland Ship Canal) or between the lakes and other drainage areas (e.g. the Miami–Erie Canal which, in 1830, reestablished connection with the Mississippi; and the Long Lac Diversion, completed in 1938, which connects Lake Superior and the Hudson Bay drainage region). Devastation of the lake trout and whitefish populations by the sea lamprey, which entered the Upper Lakes through the Welland Canal in 1932, is well known; what, if any, benthic components also extended their range must remain in the realms of speculation.

Benthic research on each of the five major Great Lakes will now be reviewed to provide a general view of the distribution and abundance of the various components discussed above.

Communities

LAKE SUPERIOR

After the first brief notes by Jackson (1844) and Agassiz (1850), benthological investigations on Lake Superior began with an intensive and reasonably extensive study by the U.S. Lake Survey in August and September of 1871 which, for the first time, provided biologists with a comprehensive and remarkably accurate view of the benthic invertebrates of one of North America's Great Lakes (Smith and Verrill 1871; Smith 1871, 1874b). Smith (1874b, p. 692) summarized the results of the survey thus: "In the shallow waters along the shores, the fauna varies with the varying character of the bottom, while below 30 to 40 fathoms (55 to 73 m), where the deepwater fauna properly begins, the same species seem to be everywhere nearly uniformly distributed down to the deepest points. The soft clayey bottom is, however, very unfavorable to most forms of animal life, and, as we might expect, the fauna of this region is very meager. Except among the worms, it seems to have scarcely any species peculiar to it, and is characterized rather by the absence of many of the shallow-water species than by forms peculiar to itself." The subsequent systematic treatment of the fauna reveals that deep water animals include *Pontoporeia affinis*, *Mysis relicta*, *Pisidium* sp., "*Chironomus*" sp., a number of oligochaetes, and a species of *Hydra*. The identity of the Oligochaeta described by Verrill (Smith and Verrill 1871) is problematical, but Michaelsen (1900) considers *Saenuris* and *Chirodrillus* to be dubious enchytraeid taxa.

Shallow water animals recorded by Smith (1874b) include the crustaceans *Cambarus bartoni* and *Hyalella azteca* (shore-dwelling), *Gammarus lacustris limnaeus* and *Crangonyx gracilis* (7 to 37 m), the lumbriculid oligochaete *Eclipidrilus lacustris* (14.6 to 23.8 m), eight species of Hirudinea, a number of insects (including Chironomidae, Ephemeroptera, and Trichoptera), about 20 species of gastropods (*Limnaea*, *Physa*, *Gyraulus*, *Valvata*, *Amnicola*, *Goniobasis*, and *Pleurocera*), 11 sphaeriids, two unionids, and the widely distributed *Hydra carnea*; it was also noted that many of these animals were associated with growths of *Cladophora*.

Despite this auspicious beginning, nearly a century elapsed before any significant advances were made on the benthic biology of the largest freshwater lake on earth.

Eddy (1943, p. 37) observed that on exposed shores, especially to the north and northwest, "...practically no organisms were found until a depth of 8 to 10 feet was reached," and that the profundal fauna, consisting of *Pontoporeia*, *Pisidium*, annelids, chironomids and nematodes, were "very abundant" between 30 and 60 m and became progressively less dense to about 275 m, below which he found only *Pontoporeia*.

Modern studies of profundal fauna of Lake Superior appropriately began with another U.S. Lake Survey which was carried out in September 1968 and was reported by Adams and Kregear (1969). On the basis of field and laboratory descriptions of the sediments, these authors distinguish three benthic environments:

1) boundary: "a zone from 2 to 10 km wide along the southern periphery of the eastern basin and portions of the eastern and western shorelines of the Keweenaw Penninsula" (p. 10), characterized by sands with median diameters from 1.2 to 3.7Φ ($\Phi = \log_2$ particle size in mm) and extending to between 60 and 90 m in depth;

2) shoal: occurring "on the tops of shallow aereally restricted positive topographic features which project to within 30 m of the water surface" (p. 15) having sands mixed with very coarse particles ($>-3\Phi$);

3) pelagic: occupying the great majority of the lake basin whose sediment surface consists of greenish-gray to reddish-brown lacustrine muds; texturally the sediments are poorly sorted and range in median diameter from 2.3 to 10.4Φ.

The important pelagic environment of Adams and Kregear (1969) is equivalent to the open-lake, deepwater zone in the previous and subsequent discussion, and was found to be dominated by *Pontoporeia affinis*, oligochaetes, chironomids, and sphaeriids. Proportions and species composition of these components differed between the three major environments as follows: *P. affinis* accounted for an average of 70% of the total fauna of the pelagic biotope, 43% in boundary sands, but only 20% on bedrock (probably present only when algal growths occurred), and 88% in the small, unstable shoal areas. Oligochaeta formed 25% of the pelagic fauna of which nearly 75% were *Stylodrilus heringianus*, and the remainder *Peloscolex variegatus* and a *Tubifex* species; about 6% of the boundary sand fauna were oligochaetes, again with *S. heringianus* dominating, but with a more diverse tubificid and naidid component consisting of *Peloscolex ferox*, *Limnodrilus* sp., *Tubifex* sp., *Nais* sp., and *Stylaria lacustris*; 43% of boundary bedrock communities consisted of Naididae, dominated by *Stylaria lacustris* with rare occurrences of *Vejdovskyella comata*, *Nais* sp., and *Chaetogaster* sp., and 10% of the shoal fauna was composed of a predatory *Chaetogaster* species. Sphaeriidae totalled 3% in the pelagic zone, 51% in boundary sands, but were completely absent from bedrock stations and the unstable shoals. Chironomidae of the genera *Heterotrissocladius* and *Chironomus* amounted to 2% of the pelagic total (C. E. Adams personal communication); the former made up 3% in boundary sands, and together with *Microtendipes* and some Orthocladiinae formed 20% of the fauna at bedrock stations. Chironomids were absent from the shoal areas. Also noted in this work was the existence of a distinct community associated with growths of algae, consisting of Naididae, Chironomidae, Hydracarina, *Asellus communis*, *Gyraulus*, *Helisoma*, and *Valvata sincera*; nematodes and a species of *Hydra* were present in significant numbers at some stations.

In a study of the Apostle Islands region, Hiltunen (1969b) found that *P. affinis* populations varied from 18 to 1935 individuals/m^2 (mean 828/m^2) and on average formed 48% of the total population. Oligochaetes consisting of *S. heringianus* (dominant), Enchytraeidae, *Limnodrilus claparedeianus*, *L. hoffmeisteri*, *L. profundicola*, *L. udekemianus* (?), *Peloscolex superiorensis*, *P. variegatus*, *Rhyacodrilus montanus*, *Tubifex kessleri americanus*, and *T. tubifex*, ranged from 8 to 1588/m^2 (mean 475/m^2) and formed 28% of the total; 0 to 1094 *Pisidium*/m^2 (mean 302/m^2) constituted 17% of the fauna, and chironomids ranging from 4 to 261/m^2 (mean 96/m^2) accounted for 6% of the total: chironomids were made up of *Calopsectra*, *Hydrobaenus*, *Microtendipes*, *Procladius*, *Tanytarsus* (*Stictochironomus*), *Tanytarsus* (*Tanytarsus*), *Protanypus*, and *Heterotrissocladius*, the latter two being primarily profundal. Total populations in Hiltunen's study ranged from 228 to 4081 individuals/m^2 with a mean of 1720/m^2, and 32 stations in the central and eastern part of the lake studied by Schelske and Roth (1973) had total populations of 14 to 1190/m^2 (mean 392/m^2).

Hiltunen's (1969b) population counts convinced Alley and Powers (1970) of the accuracy of their estimate of total standing stocks (based on six deep-water stations of eastern Lake Superior) of 0.09 g/m^2 which is very low and indicative of extreme oligotrophy.

The benthos of nearshore and harbor areas of Lake Superior have received some attention in recent years. Depth distributions and general ecological information on the benthos of north shore Goulais, Batchawana, Pigeon, and Mountain bays were presented by Thomas (1966), whose extensive species list demonstrates the diverse nature of inshore faunas; mentioned were 9 species of Hirudinea, 11 crustaceans, 30 insects, 16 gastropods, 6 unionids, and 17 sphaeriids. Oligochaetes were not identified by Thomas, but Hiltunen's (1969b) data on Chequamegon Bay, on the southwest shore, indicates that an equally rich naidid and tubificid association together with the polychaete *Manayunkia speciosa* exists in some Lake Superior bays.

Many other inshore surveys have been undertaken for the specific purpose of assessing the extent and impact of pollutants from municipalities and pulp mill industries on various north shore areas. German (1968) reported that the indigenous benthos of inner Nipigon Bay had been replaced by an association of oligochaetes (up to 2800/m^2) and chironomids (up to 360/m^2); an area within a radius of 1.6–2.4 km of Red Rock could be classified as moderately polluted, but recovery was rapid and overall the bay was dominated by *P. affinis*.

Outer Nipigon Bay was surveyed extensively by Freitag et al. (1973a), who found the order of dominance to be *P. affinis*, chironomids (mainly *Chironomus tentans*) and oligochaetes (mainly *Chaetogaster* spp.): the shallow warm waters of the western shores were dominated by gastropods and *Hexagenia*. Freitag et al. also correlated species distributions with various physical parameters and found significant inverse relations between depth and *Pisidium* species, *Amnicola limosa*, *Gyraulus* spp., *Valvata* spp., *Isotomurus* sp., and *Hexagenia limbata*; and positive correlations between sediment pH and the occurrence of *Pisidium* spp., *Valvata* spp., and *Ephemera simulans*.

A similar analysis of Thunder Bay and northern Lake Superior benthos by these same authors (Freitag et al. 1973b) established the order of dominance as *P. affinis*, chironomids, and oligochaetes, and demonstrated that the distribution of *Pisidium* species was positively correlated with depth, sediment and water Eh and water pH, and inversely related to substrate particle size; differences between their Nipigon Bay and Thunder Bay correlations are probably the result of differing specific composition of the two faunas. In contrast to the good overall situation in Thunder Bay, German's (1967) studies showed that the western part of the inner bay adjacent to the Kaministikwia River mouth, and areas within the breakwater of Lakehead Harbor, were grossly polluted and supported tubificid populations of up to 21,000/m^2; the condition of the Kaministikwia River itself can be judged by the facts that the *T. tubifex–L. hoffmeisteri* association reached 430,000/m^2 at one station, and that a macrobenthic fauna was entirely absent when wood fibres covered the bottom.

A comparable situation was described by German and Pugh (1969) in the western arm (Moberly Bay) of Jackfish Bay; pulp mill wastes had obliterated the benthos of the extreme inner part of Moberly Bay and only tubificids (up to 28,000/m^2) and chironomids existed at most other stations. In contrast, *P. affinis* was dominant in the unpolluted eastern Tunnel Bay.

LAKE HURON

Of all the Great Lakes, Huron has received the least attention from benthologists on a lake-wide basis, despite the great range of habitats it encompasses, and despite systematic work on individual groups of the Georgian Bay area reported in *Contributions to Canadian Biology*, 1911–1914 (Clemens 1915 on Ephemeroptera; Robertson 1915 on Mollusca; Sars 1915 on Entomostraca; White 1915 on Bryozoa). The only significant accounts of the deep oligotrophic main basin are those of Teter (1960), Schuytema and Powers (1966), and Shrivastava (1974); Schneider et al. (1969) surveyed shallow, eutrophic Saginaw Bay and Brinkhurst (1967) reported on oligochaetes from the same samples.

The open lake is dominated by the familiar *Pontoporeia affinis*, oligochaete, sphaeriid, chironomid association. Teter's (1960) samples from June to October 1952 and 1956 contained 81% *P. affinis*, 9% oligochaetes, 8.5% sphaeriids, and 0.5% chironomids, while corresponding figures from Schuytema and Powers (1966) based on June and August 1965 samples were 59, 22, 14, and 3%, respectively. Shrivastava (1974) found 38% *P. affinis*, 33% oligochaetes (over half of which were *Stylodrilus heringianus*), 22% sphaeriids, 4% chironomids, and 4% gastropods, between April and June 1971. It would appear that from 1952 to 1971 the proportion of amphipods in the community decreased dramatically, with a corresponding increase in oligochaetes and sphaeriids; however, direct comparisons of these figures should be approached with caution because of the different seasons at which the samples were taken, and because the three studies were based on different sampling patterns. Thus Shrivastava's figure for *P. affinis* is a spring/early summer average which will tend to be a low estimate of the potential population, because of the loss of young-of-the-year in screening samples.

In terms of total macroinvertebrate populations, Teter (1960) and Shrivastava (1974) found, respectively, an average of 2000/m^2 and 720/m^2 in deep water, and 625/m^2 and 700/m^2 in shallow water. The inverse correlation between total population size and depth which was demonstrated by Schuytema and Powers (1966) and compared with the Lake Michigan situation, is probably a reflection of the shallow, highly productive Saginaw Bay samples included in this data. The latter authors recorded 630 profundal animals/m^2, 1270/m^2 in harbor and inshore areas, 900 to 1600/m^2 in the productive channels leading from the open lake to the North Channel, and in Saginaw Bay, 4800/m^2 in spring, 2600/m^2 in summer and 3100/m^2 in the fall.

The specific composition of open lake oligochaetes was determined by Shrivastava (1974) as *Stylodrilus heringianus* (18% of the total benthos), *Limnodrilus hoffmeisteri* (4.5%), *L. profundicola* (1%), *Peloscolex ferox* (3.3%), *Tubifex tubifex* (2.2%), and *T. kessleri americanus* (0.7%), together with infrequent occurrences of *L. claparedeianus*, *P. multisetosus*, *P. freyi*, *P. superiorensis*, *Ilyodrilus templetoni*, *Potamothrix vejdovskyi*, *Aulodrilus americanus*, *Rhyacodrilus sodalis*, and *R. montana*, and the naidids *Slavina appendiculata* and *Arcteonais lomondi*. Apart from the relatively high proportion of the saprophilic *L. hoffmeisteri*, this association is similar to the oligotrophic Lake Superior fauna described by Hiltunen (1969b).

In Saginaw Bay, however, the fauna is clearly affected by the polluted Saginaw River, and the oligochaete community is dominated by *L. hoffmeisteri*, together with a somewhat eutrophic to mesotrophic assemblage consisting of *L. cervix*, *L. maumeensis*, *L. claparedeianus*, *I. templetoni*, *Peloscolex ferox*, *Potamothrix vejdovskyi*, *P. moldaviensis*, *A. americanus* and *A. pigueti* (Brinkhurst 1967). In 1956, outer Saginaw Bay benthos consisted of more or less equal numbers of oligochaetes and *P. affinis*, with *Gammarus*, *Chironomus decorus*, *C. plumosus*, *Procladius*, *Cryptochironomus*, *Pseudochironomus*, *Endochironomus*, *Calospectra*, Diamesinae spp. Orthocladinae spp., *Hexagenia*, nematodes, and isopods (Schneider et al. 1969).

The latter authors analyzed Saginaw Bay benthos samples at 50 stations taken in June to October, 1956 and compared their results with Surber's (1955) June data, and the May to September, 1965 observations of Schuytema and Powers (1966); they concluded that a catastrophe occurred in 1955 or 1956, similar perhaps to the western Lake Erie event of 1953 (Britt 1955) in which the mayfly *Hexagenia* suffered drastic and irreversible decreases (63/m^2 in 1955, 9/m^2 in 1956 and 1/m^2 in 1965): Sphaeriidae were temporarily reduced (122/m^2 in 1955, less than 1/m^2 in 1956, 100/m^2 in 1965), and oligocheates increased from 2175/m^2 in 1955 to 3530/m^2 in 1956 and 3060/m^2 in 1965.

LAKE MICHIGAN

The benthological history of Lake Michigan extends back to June 24, 1870, when an expedition on the open lake "spent the entire day dredging in a most enjoyable, and to science profitable, manner" (Hoy 1872). A cooperative effort of the Wisconsin Academy of Arts and Letters and the Chicago Academy of Science, this expedition was stimulated by Hoy's (1872) discovery of four apparently new species of crustaceans and a *Pisidium* in the gut contents of whitefish caught in deep waters. The Crustacea were examined by Stimpson (1871), who recognized *Mysis* and three species of *Gammarus* which all were later determined by Smith (1874a) as *Pontoporeia*. The expedition proved that these animals live in or on bottom deposits in large numbers, and subsequent investigations achieved little more than extending species lists, until the classical quantitative studies of Eggleton (1937) established the relation between faunal abundance and depth.

Based on 167 samples collected in the spring, summer and autumn months of 1931 and 1932 at depths ranging from 24 to 246 m, Eggleton (1937) concluded that the deeper waters of Lake Michigan were dominated by *Pontoporeia affinis* (totalling about 65% of the population), Tubificidae (24%), and Sphaeriidae (5%). Between 35 and 50 m deep a pronounced "concentration zone" existed in which the dominant organisms achieved populations between 1500 and 6250/m^2 (mean in 1931, 2709/m^2) compared with a range of 50 to 4670/m^2 (mean, 660/m^2) below 90 m; a minor peak in abundance also occurred between 100 and 140 m in both years.

Over 30 years later, Eggleton's methods were used in two major studies of the lake: the Great Lakes–Illinois River Basins Project staff of the U.S. Public Health Service conducted extensive surveys of open Lake Michigan from 1962 to 1964 (Cook and Risley 1963, Cook et al. 1965) and two inshore areas on the east shore (Cook and Powers 1964). The ongoing program of the Great Lakes Research Division at the University of Michigan has contributed many significant studies of Lake Michigan benthos dealing principally with population densities, depth distributions, and the relation of faunal subdivisions and sediment types (Robertson and Alley 1966; Powers and Alley 1967; Powers and Robertson 1968; Alley and Anderson 1968; Alley and Powers 1970; Mozley and Garcia 1972; Schelske and Roth 1973).

This recent work has confirmed most of Eggleton's (1937) results, but differences have also been detected in the relative proportions of the major components which are attributable to eutrophication processes (see below). A grand average for total fauna at all depths in 1962 and 1964, respectively is given as 4229/m^2 by Cook and Risley (1963) and 4265/m^2 by Powers and Alley (1967); Schelske and Roth (1973) were in general agreement with Powers and Alley's (1967) average proportions of the dominant fauna of 64% *P. affinis*, 20% oligochaetes, 15% sphaeriids, and 1% chironomids. In addition to the dominant groups, Cook and Risley (1963) and Cook et al. (1965) listed the following minor components of Lake Michigan benthos: *Helobdella stagnalis*, *Gammarus* sp., *Asellus* sp., 37 species of Chironomidae belonging to 14 genera, *Chaoborus* sp., Ephemeroptera, Trichoptera, Coleoptera, Hemiptera, *Valvata* sp., *Amnicola* sp., *Physa* sp., and a species of Bryozoa.

Robertson and Alley (1966) found that *P. affinis* populations tended to be concentrated at around the 40 m depth zone, with a minor peak in abundance in about 100 m of water, while Powers and Alley (1967) described a general zone of high faunal abundance between 20 to 60 m depth. The latter concluded that faunal diversity, population densities, and benthic biomass tended to decrease with increasing depth from about 20 m. Depth, however, is probably only an indirect factor involved in determining distributions and population densities, but a complex of factors which are of a more fundamental nature are intimately related to it. Thus in Lake Michigan, the gross physical structure of the bottom deposits is related to depth; the sedimentary organic carbon content tends to increase with decreasing particle size and is therefore also correlated with depth (Powers and Robertson 1968).

Cook et al. (1965) stated that organic sedimentation is particularly heavy in inshore areas along the southern and western industrial shores, and this provides a habitat more suitable for oligochaetes than amphipods. They found oligochaete populations of 16,000/m^2 between Racine and Waukegan and in the region of Milwaukee, and up to 4500/m^2 in a narrow strip between 12 to 16 km offshore in the south and southeast up to about the level of Benton Harbor. Except for areas of high productivity 32 km northeast of Chicago and 19 km east of Milwaukee, in which amphipods attained populations of 4500 and 5500/m^2, respectively, and oligochaetes 2500 and 12,000/m^2, respectively, amphipod populations tended to be high when oligochaetes were less abundant. The species composition of Lake Michigan oligochaetes was studied by Hiltunen (1967), who recorded *Stylodrilus heringianus*, 12 species of Naididae and 26 Tubificidae in the open lake, and by Howmiller and Beeton (1970) who found similar, though somewhat fewer, species in Green Bay. Results of these studies indicate that most of the Naididae, *S. heringianus*, *Peloscolex variegatus*, *Limnodrilus profundicola*, and probably *Tubifex kessleri americanus* are restricted to clean waters; that *Limnodrilus hoffmeisteri*, *L. claparadeianus*, *L. cervix*, *L. udekemianus*, *L. maumeensis*, *Peloscolex multisetosus*, *Ilyodrilus templetoni*, *T. tubifex*, and *Dero digitata* can withstand highly enriched environments; and that *Peloscolex ferox*, *P. freyi*, *Potamothrix*, and *Aulodrilus* species, together with some of the saprophilic species, form a mesotrophic association.

Eggleton's (1937) baseline information on the benthos in 1931 has been compared with the two major surveys carried out between 1962 and 1964: in terms of population densities, Robertson and Alley (1966) found that the three major components, *P. affinis*, Oligochaeta, and Sphaeriidae, had increased by factors of 1.5, 2.6, and 4.3, respectively, while Cook et al. (1965) noted that in the concentration zone (20 to 40 meters) *P. affinis* and oligochaetes had reached, respectively, 3 and 8 times their former abundance. In percentage composition, these figures are consistent with Cook and Risley's (1963) observations that *P. affinis* decreased from 60% of the total fauna in 1931 to 44% in 1962, whereas oligochaetes had increased from 24 to 39% of the total, at stations common to both surveys. All these authors attributed the observed changes to eutrophication processes; Schelske and Roth (1973) failed to detect similar changes for the period between Robertson and Alley's (1966) 1964 survey and their 1970 data.

The documented changes in the fauna of Green Bay are undeniably a consequence of increasing pollution loads from the Fox River. Howmiller and Beeton (1971) compared Surber and Cooley's (1952) data with their 1969 findings, which were based on samples taken at the same stations, at the same time of the year, and employing similar methods. Between 1952 and 1969 the abundance and proportion of oligochaetes (species composition documented in Howmiller and Beeton 1970) had increased generally over the whole bay (66 to 85% in the lower bay, 23 to 64% in the middle bay) while amphipods, leeches, gastropods, sphaeriids, and *Hexagenia* had disappeared or undergone drastic declines. Increased numbers of Chironomidae were observed at most stations, but overall they had declined in relative importance from 37% in 1952 to 26% in 1969.

Cook and Powers (1964) reported similar but far less drastic trends in a comparison between the lake fauna adjacent to Benton Harbor at the mouth of the St. Joseph River, which contributes 3–4 thousand tons of suspended solids to the lake annually, and a similar area around Little Sable Point, which has no major tributaries near it. Total counts of benthos were, respectively, 5542/m^2 and 4918/m^2; amphipods contributed 34 and 72% of the total, oligochaetes 57 and 15%, sphaeriids 7 and 8%, and chironomids 2 and 5%, respectively.

In a detailed study of species composition and abundance of nearshore benthos about 16 km south of Benton Harbor, Mozley and Garcia (1972) recognized three faunal zones imposed on a gradient of increasing total abundance from 4 to 25 m (compare the general inverse correlation between depth and abundance below 25 m): (1) the beach zone (4 to 6 m where the fauna was composed predominantly of the chironomids *Parachironomus* nr. *demeijerei*, *Paracladopelma* nr. *nereis*, *Chironomus fluviatilis*-group, and *Cryptochironomus* sp.; (2) from 8 to 15 m *Pontoporeia affinis*, *Limnodrilus hoffmeisteri*, and *Sphaerium striatinum* dominated, but *Potomothrix moldaviensis* and *Polypedilum* nr. *scaleanum* characterized the zone; (3) between 20 to 25 m large numbers of *Stylodrilus heringianus* and *P. affinis* occurred together with *Sphaerium nitidum*, *Pisidium* spp., *Procladius* sp., *Chironomus anthracinus*-group, and *Helobdella stagnalis*. These faunal divisions were found to correspond with physically recognizable zones of different sediment types whose characters are probably determined chiefly by prevailing currents and wave action.

LAKE ERIE

Major changes have occurred in the bottom fauna of Lake Erie, particularly in the highly eutrophic western basin, where there have been many studies. Information is scanty on the central and eastern basins.

In the period 1928–30, Wright (1955) attempted to determine effects of a growing pollutant load in the western basin on the decline of commercially important fishes. Although close to 60% of the total numbers in the main groups were oligochaetes, the burrowing mayfly *Hexagenia* accounted for 12% (139/m^2) and molluscs averaged 25% of the total of 1150/m^2.

A more detailed study was carried out by Shelford and Boesel (1942) in the region of Gibralter Island to a depth of about 6 m. They identified three community types: the *Goneobasis–Hydropsyche* community on areas swept clear of sand and silt by wave action and currents, the *Pleurocera–Lampsilis* community characteristic of sandy bottoms, and the *Hexagenia–Oecetis* community of mud-bottom areas. The latter contains many chronomid larvae, molluscs, amphipods, and oligochaetes. Although these assemblages are named simply after the common species present, and may have little other significance, the diversity in the communities (as shown in their extensive species lists) is impressive.

Wood (1963) employed a drag-dredge to sample benthic macroinvertebrates in 1952; he converted data to areal abundance by trial comparisons of his gear with the Ekman dredge. He collected 685 animals/m^2, 235 or 34% of which were *Hexagenia* nymphs and 169 or 25% molluscs. The oligochaetes were not included by Wood, which would account for much of the difference from Wright's populations estimates. The species diversity in Woods' samples was obviously great, and indicates, in comparison with other earlier studies (e.g. Shelford and Boesel 1942), that water quality was fair until 1952. However, dramatic changes in the benthic macroinvertebrate community in western Lake Erie occurred in 1953. A prolonged period of calm weather in the summer of 1953 led to persistent thermal stratification and severe depletion of oxygen in the hypolimnion. Afterwards, Britt (1955) found only 44 live mayfly nymphs/m^2, compared with about 400/m^2 in earlier studies. Some recovery occurred during the following year but Carr and Hiltunen (1965) found less than 2/m^2 in the open lake area in 1961. Carr et al. (1965) described the increasing frequency and severity of periods of oxygen depletion in the western basin of Lake Erie.

One of the most informative studies on benthic macroinvertebrates of the St. Lawrence Great Lakes, in our opinion, is that by Carr and Hiltunen (1965) carried out in 1961 at Wright's stations. The fauna in 1961 was composed principally of oligochaetes (5949/m^2 and 80% of the total), chironomids (322/m^2), sphaeriids (438/m^2), and gastropods (221/m^2). Oligochaetes were almost nine times as abundant in 1961 as in 1930; chironomids were four times, shaeriids twice, and gastropods five times as abundant in 1961 as in 1930. Numbers of oligochaetes were highest, 13,000 to almost 40,000/m^2 near the mouth of the Detroit River, and exceeded 10,000/m^2 near the mouths of the Raisin and Maumee rivers. Wright (1955) had categorized the 1931 samples as heavily and moderately polluted on the basis of oligochaete numbers, in excess of 5000/m^2 for the former, 1000–5000/m^2 for the latter. Carr and Hiltunen (1965), using the same criteria, compared their results with those of Wright to show the expansion of the impact of pollution on western Lake Erie (Fig. 1). The most abundant oligochaetes are *Limnodrilus hoffmeisteri*, *L. claparedeianus*, *L. cervix*, and *L. maumeensis*, with *Tubifex tubifex* apparently restricted to the area of the mouth of the Detroit River (Brinkhurst et al. 1968). The zone of moderate pollution increased from 46 km^2 in 1930 to 517 km^2 in 1961, while the area heavily polluted increased from 26 km^2 to 238 km^2. The total area classified as polluted in 1930 was 263 km^2 (26% of the study area), but in 1961 all 1020 km^2 were considered polluted — 26% lightly, 51% moderately, and 23% heavily polluted.

Molluscs were scarce or apparently absent in the Maumee Bay area and along the western shore; they were most abundant offshore and many species appear to have increased in abundance between 1930 and 1961. The snail *Valvata sincera* was most abundant in the inshore polluted areas, and in comparison with earlier reports the species apparently has increased in abundance and widened its distribution during the decade 1951–60. Similarly, the sphaeriid *Sphaerium transversum* appeared to be rather tolerant of declining water quality. The naiads were confined almost exclusively to the deeper, offshore waters to depths as great as 10 m, where normally they would be expected to be less abundant than in shallow, inshore waters. Only three genera of chironomids were wide-spread — *Procladius*, *Coelotanypus*, and *Cryptochironomus* species. In summary, the decrease in mayflies and the increase in oligochaetes and chironomids were the most striking and widespread changes which took place during the 31 years between these two studies. Also, the 1967 study by Veal and Osmond (1968) had findings similar to those of Carr and Hiltunen, with close agreement on oligochaetes and presence of other associated species (except that no *Hexagenia* and no caddis larvae were collected).

Less information is available on benthic macroinvertebrates of the central and eastern basins compared with western Lake Erie. However, sufficient data exists in reports by Brinkhurst et al. (1968) and by Veal and Osmond (1968) to demonstrate the shift through three associations from west to east. The *Limnodrilus* spp. association of the western basin includes a variety of associates from other groups (e.g. *Valvata sincera*, several sphaeriids, the chironomids *Procladius bellus, Coelotanypus concinnus*, *Cryptochironomus* sp., and *Chironomus plumosus*). Farther out the western basin other species enter the community, including *Aulodrilus* spp. and *Potamothrix* spp., together with *Branchiura sowerbyi*, *Pelscolex multisetosus*, and *P. ferox*. The latter species is the most abundant oligochaete in the central basin, whereas *Stylodrilus heringianus* and *Tubifex tubifex* were the main oligochaetes in the eastern basin; *S. heringianus* has not been collected from the western basin. The chironomids *Heterotrissocladius sudpilosus*, *Tanytarsus* sp., *Micropsectra* sp., *Monodiamesa* cf. *bathyphila*, and *Potthastia longimanus*, commonly considered indicative of more oligotrophic conditions, were found in the eastern basin (Brinkhurst et al. 1968). The amphipods *Pontoporeia affinis* and *Gammarus* (probably *G. fasciatus*) amounted to 27% of total numbers of macroinvertebrates in the eastern basin to about 10 km off the Canadian shore (Veal and Osmond 1968), compared with only 6% of total numbers in the central basin. Conversely the percentage of oligochaetes decreased from 86% in the western basin to 55% in the central basin to 34% in the eastern basin. Total macroinvertebrate numbers were 7500/m^2, 2400/m^2, and 4600/m^2 in the western, central, and eastern basins, respectively.

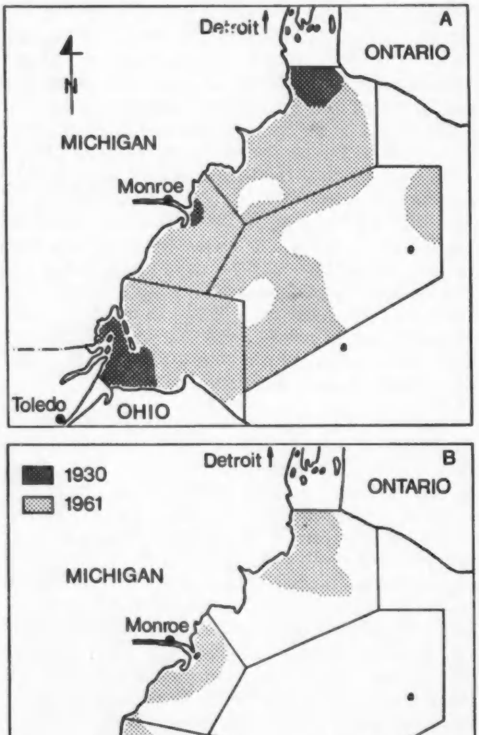


FIG. 1. Comparison of zones of pollution in western Lake Erie, 1930 and 1961, redrawn from Carr and Hiltunen (1965). A, Zones of moderate pollution (1000–5000 Oligochaeta/m^2); B, Zones of heavy pollution (more than 5000 Oligochaeta/m^2).

LAKE ONTARIO

The results of two studies on Toronto Bay, carried out close to 100 years apart, stand in stark contrast, documenting as they do one of the greatest local declines in Great Lake's water quality on record. Nicholson (1873) described the macroinvertebrate fauna as follows: "The greater proportion of the Bay, comprising the central portion of its area, appears to consist uniformly of a tenacious, bluish-gray, exceedingly fine grayish mud... it contains numerous small Annelides of the genus *Saenuris* along with many larvae of a Dipterous insect allied to *Chironomus*... the latter being very conspicuous from their brilliant red colour. Towards the edges of the Bay, where the depth diminishes to one and a half fathoms or less, the bottom consists of sand, covered over considerable areas with a dense growth of weeds of different kinds. The chief varieties of bottom in this shallow zone are the following: — 1. pure siliceous sand with dead shells... 2. sandy mud with a dense growth of *Charas*, containing numerous *Gammari*, small leeches, larvae of *Chironomus* and Ephemerids, with the shells of *Unio*, *Cyclas*, *Pisidium*, *Paludina*, *Planorbis*, *Physa*, *Melania* and *Valvata*. 3. Sandy mud, sometimes with peaty layers, supporting a luxuriant vegetation of *Anacharis Canadensis* and *Charea*... the sand was crowded with *Uniones*, the dredge coming up completely packed with living and dead shells."

Brinkhurst's (1970) present-day description is one of exceptional (even by contemporary standards) populations and standing stocks of oligochaetes, "in excess of 200,000/m^2" and varying from 42.7 g/m^2 along the industrial shore to 4.3 g/m^2 by the opposing island shore.

In October 1922, Adamstone (1924) secured a limited series of Ekman-dredge samples between Toronto and the Niagara River. The average population of all animals was 1500/m^2, which is less than populations described more recently.

Studies carried out over the past decade include the work by Johnson and Matheson (1968) in Hamilton Bay, by Hiltunen (1969c) and Kinney (1972) over the entire lake, and by Brinkhurst (1970) in Toronto Bay and Johnson and Brinkhurst (1971a, b, c) in the Bay of Quinte and eastern Lake Ontario.

Populations in the deep basin, in excess of 90 m deep, averaged 2600 in Hiltunen's study and 1100/m^2 in Kinney's work. In each case about 50% of animals collected were *Pontoporeia affinis* and 30% were oligochaetes, of which close to two-thirds were *Stylodrilus heringianus*. *Tubifex tubifex* and *Limnodrilus hoffmeisteri* accounted for most of the remaining oligochaetes, but *Limnodrilus profundicola*, *Tubifex kessleri americanus*, *Rhyacodrilus* sp., *Peloscolex variegatus*, *P. ferox*, and *P. multisetosus* have been taken in deep sediments. The most abundant chironomid taken in the deep zone is *Heterotrissocladius subpilosus*, with much smaller relative numbers of *Micropsectra* sp. and *Procladius* sp. Johnson and Brinkhurst (1971a) listed these deep-water species as *Micropsectra* nr. *dives* and *Procladius denticulatus*. Sphaeriids are not abundant in the deep zone, but *Pisidium conventus* penetrates to the extreme depths in Lake Ontario (Hiltunen 1969c).

Populations increase toward shallower sediments; Kinney (1972) collected about 4400/m^2 in the 42–78 m zone, with approximately equal numbers (40% of the total for each) of *Pontoporeia affinis* and oligochaetes, about equal in abundance to *Limnodrilus hoffmeisteri*. Some rare species in the deep zone, plus others, assumed greater importance, such as *Peloscolex ferox*, *P. variegatus*, *Rhyacodrilus* spp including *R. montana*, *Potamothrix moldaviensis*, and *P. vejdovskyi*. A more diversified midge fauna occurs in this zone and includes *Chironomus* spp. *Tanytarsus* sp., *Micropsectra* sp., and *Procladius* sp., as well as *H. subpilosus*. The snails *Valvata sincera* and *V. tricarinata* also penetrate into the 42–78 m depth range.

Local differences in species composition can be detected in this intermediate-depth zone. In the Niagara and Oswego areas Kinney (1972) found reductions in the numbers of *Stylodrilus heringianus*, increases in numbers of tubificids, including such species as *Peloscolex ferox*, *P. multisetosus*, *Potamothrix moldaviensis*, *P. vejdovskyi*, *Limnodrilus claparedeianus*, *L. udekemianus*, and the dominance of *L. hoffmeisteri* and *Tubifex tubifex*. Complete absence of the usual dominants *Pontoporeia affinis* and *Stylodrilus heringianus* was shown off the Niagara River mouth. Such differences, as noted above, cannot reasonably be attributed to depth, but are related to characteristics of sediments and water quality.

The impact of declining water quality is more obvious in the shallow zone, to 48 m in Hiltunen's analysis, to 36 m in Kinney's work, and to 20 m in western Lake Ontario in the study by Johnson and Matheson (1968). Actually, the task of determining the so-called natural fauna of the nearshore zone is rather difficult. Generally, as observed along the least affected of the Lake Ontario shoreline, the natural assemblage apparently consists of approximately equal numbers of the dominant *Pontoporeia affinis*, *Stylodrilus heringianus*, *Limnodrilus hoffmeisteri*, and *Tubifex tubifex*, plus a variety of chironomids and sphaeriids in much lower numbers.

Macroinvertebrate communities near the mouths of Hamilton Bay, the Bay of Quinte, Niagara River, Genesee River, and Oswego River indicate in varying degrees the effects of waste inputs. The oligochaete *Tubifex tubifex* was found in western Lake Ontario only in the "plume" of richer sediments projecting from Hamilton Bay; *Chironomus attenuatus* was the dominant chironomid locally, and sphaeriids were less abundant in the plume than elsewhere in the vicinity (Johnson and Matheson 1968). The community in Prince Edward Bay, offshore from the mouth of the Bay of Quinte, had abundant *Pontoporeia affinis*, a varied chironomid and sphaeriid fauna, and, although *Stylodrilus heringianus* appeared to be restricted in its distribution, the oligochaete community was diversified and much like oligochaete associations in other less-affected parts of the Lake. The pollution-tolerant *Limnodrilus* spp. group (*L. cervix*, *L. claparedeianus*, *L. udekemianus*) was virtually absent (Johnson and Brinkhurst 1971a). Samples taken off the Niagara River mouth yielded exceptionally high numbers of oligochaetes, with *Potamothrix moldaviensis* and *Limnodrilus hoffmeisteri* (flat-plate variant) all abundant, plus all of the tolerant *Limnodrilus* spp. group (listed above) together with *Tubifex ignotus*, *Peloscolex multisetosus*, and *P. ferox*. Near the mouth of the Genesee River, samples contained relatively few *Stylodrilus heringianus* (only 6% of oligochaete numbers) but large numbers of *Limnodrilus cervix* and *L. hoffmeisteri*. Sampling near the Oswego

River mouth showed high numbers of tubificids and the infrequent occurrence of intolerant forms including *Stylodrilus heringianus* and *Pontoporeia affinis*. Conditions at this site were not sufficiently severe to preclude the existence of such common tubificids as *P. vejdovskyi*, *P. moldaviensis*, and *Aulodrilus pluriseta* or the amphipod *Gammarus fasciatus*.

The shallow water zone, as arbitrarily defined above, is a zone of comparatively large populations and species diversity. Hiltunen collected an average of 16,300/m², Kinney's samples averaged 8300/m², and Johnson and Brinkhurst found 8350/m² in Prince Edward Bay.

Many harbors and bays of Lake Ontario have been severely polluted; most of their macroinvertebrate communities were examined during the period 1964–70. Two types of macroinvertebrate communities develop, the first in shallower, mixed bays and the second in deeper, stratified waters. In the first type, exemplified by the inner Bay of Quinte (Johnson and Brinskhurst 1971a), large populations of chironomids develop (mainly *Chironomus plumosus*, *C. attenuatus*, *Procladius* spp., *Coelotanypus*) and tubificids are less abundant. In stratified waters, the *Limnodrilus* spp. community develops (*L. cervix*, *L. claparedeianus*, *L. hoffmeisteri*, *L. udekemianus*) often with few other associated invertebrates. The tolerant *Tubifex tubifex* often occurs in this group but is not always equally abundant. The species *Peloscolex multisetosus* is often associated in substantial numbers, for example in Toronto Bay (Brinkhurst 1970). The report by Johnson and Matheson (1968) of *Limnodrilus profundicola* (one specimen) in Hamilton Bay is now found, following reexamination of the specimen, to be a doubtful record. Hiltunen's (1969c) conclusion was that this species is by no means part of the *Limnodrilus* association of polluted waters. When chironomids occur, apparently reflecting somewhat better water quality than in their absence, they are usually of the groups *Chironomus* spp. (probably often *C. attenuatus*), *Procladius* spp., and *Cryptochironomus* spp. These are found in and near the mouth of Hamilton Bay (Johnson and Matheson 1968) and in Great Sodus Bay (Kinney 1972). Invertebrates of other groups which may be present (indicating a further improvement in water quality) are the crustaceans *Gammarus fasciatus* and *Asellus racovitzae*, and molluscs *Valvata* spp. and *Bithinia tentaculata*. Kinney (1972) found a community with these additions in the Rochester Embayment area (which is not an enclosed bay, but circulation into Lake Ontario is quite restricted). Although oligochaete numbers were moderate, low numbers of *L. cervix*, *L. claparedeianus*, *L. maumunsis*, and *Peloscolex multisetosus* were collected, together with *Gammarus fasciatus*, *Asellus* sp., and *Bithinia tentaculata*; however, neither *Stylodrilus heringianus* nor *Pontoporeia affinis* were collected.

The total numbers of animals in bays and harbor sediments in Lake Ontario vary widely; for example, about 2000/m² and as high as 52,000/m² in Hamilton Bay (Johnson and Matheson 1968), 50,000/m² commonly and to over 200,000/m² in Toronto Bay (Brinskhurst 1970), and to 21,000/m² in Oswego Harbor and River (Kinney 1972).

Biomass and Production

Studies providing data on biomass and production in benthic macroinvertebrate communities of the Great Lakes are so scarce that detailed synthesis is not particularly profitable at this time. Standing stocks (dry weights) are lowest in Lake Superior at 0.09 g/m² (Alley and Powers 1970) and highest in at least some enriched bays of the lower lakes, for example, Toronto Bay with 4.3 to 42.7 g/m². Average standing stocks in other lakes were 3.40 g/m² in Lake Michigan, 1.48 g/m² in Lake Huron, 4.63 g/m² in Lake Erie (Alley and Powers 1970), and 1.84 g/m² in Lake Ontario (Johnson and Brinkhurst 1971). These standing stocks may be compared with values from Canadian lakes whose trophic levels were defined by Rawson (1953), whereby Lake Superior is the only truly oligotrophic lake; Lake Huron, Lake Ontario, and eastern Lake Erie are mesotrophic; Lake Michigan is moderately eutrophic; and western Lake Erie is highly eutrophic.

Categorization of whole lakes is of general value but tends to ignore the variation in shallow water areas, especially bays, in any given lake. For example, the Bay of Quinte is a large, eutrophic bay of mesotrophic Lake Ontario. Also, the biomass of benthic macroinvertebrates, as of other elements of communities, is only crudely indicative of true production and lake productivity. Johnson and Brinkhurst (1971a, b, c) examined biomass and production in the Bay of Quinte and eastern Lake Ontario in some detail. Standing stocks were not large in the upper bay (about 1 g/m²), but annual production was close to seven times average biomass. The lower bay (Adolphus Reach) was most productive, with 20 g/m² produced annually at one station and 7.5 g/m² at a second. Standing stocks were 5.5 and 4.3 g/m².

In Lake Ontario's main basin, with a standing stock of about 2 g/m², production was estimated to be only 2.5 g/m² annually. Turnover ratios of macroinvertebrates were closely related to annual mean temperature, although turnover ratios of taxonomic groups varied. Temperature apparently had a fundamental controlling influence on turnover ratio, as it affected the metabolism of individual annuals. That is, biomass appeared to be adjusted to utilizable import of detrital food consistent with a turnover ratio set by temperature (Johnson and Brinkhurst 1971b). This generalization is probably sufficiently accurate to provide first-order estimates of production in other situations — for example, the near equality of biomass and production in deep, cold basins. Therefore, annual production of benthic macroinvertebrates in Lake Superior offshore sediments is probably close to 0.1 g/m^2/yr. In lakes Huron and Ontario, production is expected to be within 1.5–2.5 g/m^2/yr, and in lakes Michigan and Erie as high as 5.0 g/m^2/yr. Many local areas in the Great Lakes presumably have much greater production than these lakewide estimates, as shown by the lower Bay of Quinte data (7.5 to 20 g/m^2/yr). Furthermore, it is conceivable that production over much of Toronto Bay is as great as 100 g/m^2/yr. If this is probable, then production by benthic macroinvertebrate communities in the Great Lakes spans three orders of magnitude.

Discussion

MAJOR COMMUNITIES

A complex shallow water region (defined here as 0 to 70 m) encircles the lakes and includes western Lake Erie and other significantly large areas such as Saginaw Bay (Huron), Green Bay (Michigan), Bay of Quinte and Prince Edward Bay (Ontario); it should be considered more properly as a continuum, variously characterized by a combination of factors such as depth, substrate type and nutrient content, vegetation, wave or current action, and local topography. This zone is so poorly understood that any analysis incorporating these factors is impossible. However, it is important that researchers appreciate the great importance of this zone and recognize current opportunities to gain immensely from ongoing studies by geologists, physical limnologists, and sediment chemists.

The profundal zone begins at about 70 m and encompasses most of the area of the Great Lakes. From the discussion of communities in each of the major lakes, a general picture of the profundal benthos emerges as a massive system dominated by ***Pontoporeia affinis***, together with a varying number of species of Oligochaeta, Sphaeriidae, and Chironomidae. With the exception of a few rare carnivorous chironomids, the macroinvertebrate community consists exclusively of detritivorous species. It is perhaps a measure of the complexity of the system that so many different taxa are capable of exploiting the benthic environment in a constraining and superficially uniform area. The proportions in which various components occur within the community, the specific composition of the oligochaetes, sphaeriids, and chironomids, and the total numbers and biomass of the macroinvertebrates vary throughout the system in broadly recognizable patterns. We can attempt no more than a general and simplified analysis of these patterns because of the unresolved difficulties in comparing data gathered at different seasons, with various sampling devices, and employing diverse sorting and enumeration techniques.

In terms of the relative proportions of taxa, the upper lakes may be considered as a major subdivision of the system, with summer averages of 60–80% *P. affinis*, 10–20% oligochaetes, 5–15% sphaeriids, and 0–5% chironomids. Oligochaetes assume greater importance in Lake Ontario (about 50% *P. affinis*, and 30% oligochaetes) and are dominant in the eastern basin of Lake Erie (27% *P. affinis*, 34% oligochaetes). The proportion of oligochaetes tends to increase relative to *P. affinis* along a natural gradient from Lake Superior through lakes Huron, Michigan, and Ontario. Shallow, eutrophic Lake Erie is exceptional and will be discussed separately below. Total population, in numbers and biomass, formerly tended to increase along this gradient also, but Lake Michigan now has exceptionally high standing stocks which have been attributed to eutrophication processes. However, the limited watershed of southern Lake Michigan, much of which is urbanized, and consequently the low flushing rate, may account for the pronounced impact of cultural eutrophication and greater natural productivity as well.

The increasing population densities and standing stocks, and the increasing oligochaete component as one descends from the upper to the lower lakes, correlate well with two chemical gradients. Superior, Huron, Ontario, and Michigan contain, respectively, 46, 82, 93, and 113 parts per thousand of inorganic carbonate (Chandler 1964) which reflects the tendencies in standing stock values. Robertson and Powers (1967) presented figures for dissolved organic matter in Superior, Huron, Michigan, and Ontario of 2.62, 2.71, 4.91, and 6.13 mg/liter, respectively, and for particulate organic content 0.43, 0.71, 1.12, and 1.41 mg/liter, respectively, which both correlate with increasing oligochaete representation in the bottom fauna.

Lake Erie is unique because of its shallow, saucer-like basin. The entire western end formerly possessed a shallow-water community dominated by *Hexagenia* and a number of pelecypod taxa, which by the 1960s had changed to a highly eutrophic association dominated by Tubificidae. The proportion of oligochaetes decreases from 86% in the west to 55% in the deeper central region and 34% in the truly profundal eastern basin. This change in benthic composition reflects the improvement in water quality from west to east, and the lake may be visualized, in one water mass, as a reversed model of tendencies inherent in the Great Lakes as a whole. It is instructive, therefore, to examine specific composition of benthic components of different regions of the lake in more detail, and to indicate how these observations relate to communities in the four other lakes.

The oligochaetes of western Lake Erie consist predominantly of the saprophilic tubificids *Limnodrilus hoffmeisteri*, *L. cervix*, *L. claparadeianus*, and *L. maumeensis*; this highly eutrophic association, usually together with *Tubifex tubifex* and *Peloscolex multisetosus*, is common in many polluted harbor and bay areas throughout the lakes. Further east the community acquires *Aulodrilus* and *Potamothrix* species, which, with the dominant *Peloscolex ferox*, constitute the central basin fauna. The last three taxa can be considered as part of a mesotrophic association which is found also in southern Lake Michigan, much of Green and Saginaw bays, and a broad inshore zone around Lake Ontario. Eastern basin profundal oligochaetes consist of the ubiquitous *T. tubifex* and the lumbriculid *Stylodrilus heringianus*; the latter is dominant in the deep basins of all the lakes and apparently forms an oligotrophic association with such species as *Tubifex kessleri americanus*, *Peloscolex superiorensis*, *P. variegatus*, and *Rhyacodrilus* species.

Hamilton (in Brinkhurst et al. 1968) presented data on chironomid fauna of the three regions of Lake Erie. In the western basin only the resistant *Coelotanypus* nr. *concinnus*, *Chironomus* spp., *Procladius* nr. *denticulatus*, *Crypotochironomus* sp., and *Microtendipes* nr. *pedellus* can exist, and this association may be considered roughly analogous to the *Limnodrilus* association. Small numbers of the less tolerant taxa *Stictochironomus*, *Paralauterborniella* nr. *nigrohalteralis*, *Tanytarsus*, *Micropsectra*, and *Paracladopelma* nr. *obscura* enter the community in the central basin. While the resistant *Chironomus* and *Procladius* species remain dominant, taxa such as *Xenochironomus*, *Ablabesmyia*, *Demicryptochironomus*, *Monodiamesa* nr. *bathyphila*, *Potthastia* nr. *longimanus*, and *Heterotrissocladius* nr. *subpilosus* are found in the eastern basin. The latter species occur throughout the cold deep basins of the Great Lakes; *H. subpilosus*, *Tanytarsus*, *Microspectra*, *Monodiamesa*, and *Potthastia* are generally considered to be indicative of more oligotrophic conditions.

Pisidium conventus is the only sphaeriid found regularly in the deep, cold, profundal habitats of the upper lakes. Depth and temperature appear to be important factors determining the distribution of most other Sphaeriidae, but because sphaeriid identification is not done by most investigators, few general trends can be determined at present. However, *P. casertanum*, *P. compressum*, *P. nitidum*, *S. corneum*, *S. transversum*, and *S. striatinum* are common in western Lake Erie (Carr and Hiltunen 1965) and are therefore tolerant of eutrophic conditions.

OLD WORLD COMPARISONS

In terms of the species composition and proportional representation of taxonomic groups, the Great Lakes profundal benthos bears a strong resemblance to that of north European lakes. For example, Åhrén and Grimås (1965) reported that the benthos of the Ullevifjärden basin of Lake Mälaren (central Sweden) was composed of 60% *P. affinis*, 10% oligochaetes (*Peloscolex ferox*, *Limnodrilus udekemianus*, *Tubifex tubifex*, *Potamothrix hammoniensis* and *Psammoryctides albicola*), and 7% chironomids. In the polluted Ekoln basin of the same lake, amphipods had been mostly replaced by an oligochaete fauna (74%) with chironomids (8.3%) and nematodes (7.3%). Apart from the absence of sphaeriids, the latter is close to the Lake Erie situation, whereas the former is comparable to the upper lakes in terms of faunal proportions.

In general, eutrophic and mesotrophic oligochaete associations are similar on both sides of the Atlantic. The oligotrophic deep basin community dominated by *Stylodrilus heringianus* is more unusual, however. The latter belongs to the phylogenetically ancient Lumbriculidae (Brinkhurst and Jamieson 1971) which are extremely successful in old deep lakes (e.g. Lake Baikal and some of the Baltic lakes), whereas Tubificidae evolved more recently and possibly in warmer waters; thus Bousfield's remarks on the dominance of ancient Crustacea in deep, cold waters (quoted in Frey 1965, p. 626) may well apply to this case also.

Chironomid communities also bear strong affinities in the Nearctic and Palaearctic. Brundin (1951) showed that increasing tolerance to oxygen depletion is directly related to decreasing body size and the presence of the blood pigment erythrocruorin; thus on both sides of the Atlantic, *Heterotrissocladius subpilosus*, *Monodiamesa*, *Protanypus*, and *Tanytarsus* are typical residents of oligotrophic waters, whereas the series *Stictochironomus*, *Chironomus*, *anthracinus*, and *C. plumosus* exhibit increasing tolerance to eutrophic conditions.

THE FUTURE

The composition of benthic fauna has long been considered a good indicator of water quality because, unlike planktonic organisms, components form relatively stable communities in the sediments which integrate changes over long time intervals, and which reflect characteristics of both the sediments and the water column. However, biologists have encountered many problems in obtaining baseline information on natural communities and comparing this accurately with altered associations, because of the lack of good standardized sampling and sorting methods. Add to this taxonomic difficulties encountered with many of the components, problems of obtaining the many physical and chemical data properly required to correlate with observed distributions and abundances, the time-consuming nature of such work, and the large data matrices generated, it is easy to appreciate why benthos studies are somewhat unpopular.

The team approach, in which benthic work is integrated with other biological, geological, and chemical investigations, and the introduction of computer programs capable of digesting large bodies of data and searching extensive data bases for comparative purposes, have resolved some of these problems. However, sampling methodology still requires much thought, and taxonomic investigations must continue or be initiated on many benthic components. Specific areas requiring attention include basic studies on inshore components and many small and often obscure interstitial or microbenthic groups, and the correlation of juvenile and adult stages of many insects, including especially the Chironomidae. We cannot overemphasize the fundamental importance of the classical taxonomic approach which, although often considered of low priority or of secondary interest, or openly denigrated as an exercise for an outmoded generation of biologists, delineates and characterizes the basic units with which all of biology is concerned.

After, or in conjunction with, the many vital taxonomic studies, we believe that work in the following areas of benthic research should be initiated or expanded. The role of microinvertebrates and bacteria in the sediments, ecology of exposed littoral zones, and the inshore *Cladophora* community, all require basic investigation. Despite the rigorous winter in the Great Lakes basin, full seasonal studies of individual taxa and whole communities can be and need to be conducted. Little is known about the "rain" of detritus on which the benthos largely depends; integrated studies of seasonal rhythms of benthic and planktonic communities with the amount and type of this "rain" (size, taxonomic and chemical composition, which was so successfully applied by Jonasson (1972) to a study of Lake Esrom, should be initiated. Biomass determinations should be made routinely, as seems to be the case in Russian institutions (e.g. Mitropol'skii and Luferov 1966; Poddubnaya 1966), so that benthic productivity and energy flow within the benthos and between the benthos and other subsystems can be realistically discussed.

Benthic interactions with other communities (phytoplankton, zooplankton, fish) seem to us a particularly important but sadly neglected field of endeavor. For example we know little of the ecology of economically important fish spawning beds which occur in the inshore zone where benthic communities and environmental conditions are most diverse. The benthos is a rich food resource for many fish, but we do not understand the effects on fish populations of alterations in the proportions of benthic components such as shifts from *P. affinis* to oligochaetes, or *Hexagenia* to oligochaetes. Such shifts in species composition are attributable to deteriorating water quality, and although these community changes have been used successfully to detect and assess eutrophication impact, interactions between communities are not usually considered. Whatever the approach of emphasis, only continued systematic and ecological work, with intercommunity and interdisciplinary studies of the sort outlined above, will provide the data and the stimulus to establish realistic water quality standards based on whole systems and their constituent communities.

Acknowledgments

Our thanks to A. H. Clarke (N.M.C., Ottawa) for valuable advice on the molluscs. Errors of fact or omission are to be attributed to the senior author.

ADAMS, C. E., AND R. D. KREGEAR. 1969. Sedimentary and faunal environments of eastern Lake Superior. Proc. 12th Conf. Great Lakes Res. 1969: 1–20.

ADAMSTONE, F. B. 1924. The distribution and economic importance of the bottom fauna of Lake Nipigon with an appendix on the bottom fauna of Lake Ontario. Univ. Toronto Stud., Biol. Ser. No. 25, Publ. Ont. Fish. Res. Lab 24: 35–100.

AGASSIZ, L. 1850. Lake Superior: its physical character, vegetation, and animals, compared with those of other and similar regions. Gould, Kendall and Lincoln, Boston, Mass. 428 p.

ÅHRÉN, T., AND U. GRIMÅS. 1965. The composition of the bottom fauna in two basins of Lake Mälaren. Inst. Freshwater Res. Drotthingholm Rep. 46: 49–57.

ALLEY, W. P., AND R. F. ANDERSON. 1968. Small-scale patterns of spatial distribution of the Lake Michigan macrobenthos. Proc. 11th Conf. Great Lakes Res. 1968: 1–10.

ALLEY, W. P., AND C. F. POWERS. 1970. Dry weight of the macrobenthos as an indicator of eutrophication of the Great Lakes. Proc. 13th Conf. Great Lakes Res. 1970: 595–600.

Berry, E. G. 1943. The Amnicolidae of Michigan: distribution, ecology, and taxonomy. Misc. Publl. Mus. Zool. Univ. Mich. 57: 1–68.

Bousfield, E. L. 1958. Freshwater amphipod crustaceans of glaciated North America. Can. Field Nat. 72: 55–113.

Brinkhurst, R. O. 1963. Taxonomical studies on the Tubificidae (Annelida, Oligochaeta). Int. Rev. Gesamten Hydrobiol. Syst. Beih. 2: 7–89.

1965. Studies on the North American aquatic Oligochaeta II: Tubificidae. Proc. Acad. Nat. Sci. Phila. 117: 117–172.

1967. The distribution of aquatic Oligochaeta in Saginaw Bay, Lake Huron. Limnol. Oceanogr. 12: 137–143.

1969. Changes in the benthos of Lake Erie and Ontario. Bull. Buffalo Soc. Nat. Sci. 25: 45–71.

1970. Distribution and abundance of tubificid (Oligochaeta) species in Toronto Harbour, Lake Ontario. J. Fish. Res. Board Can. 27: 1961–1969.

Brinkhurst, R. O., A. L. Hamilton, and H. B. Herrington. 1968. Components of the bottom fauna of the St. Lawrence, Great Lakes. Univ. Toronto Great Lakes Inst. No. PR 33: 1–49.

Brinkhurst, R. O., and B. G. M. Jamieson. 1971. Aquatic Oligochaeta of the world. Oliver and Boyd, Edinburgh. 860 p.

Britt, N. W. 1955. Stratification in western Lake Erie in the summer of 1953: effects on the *Hexagenia* (Ephemeroptera) population. Ecology 36: 239–244.

Brown, E. H. 1953. Survey of the bottom fauna at the mouths of ten Lake Erie south shore rivers. Ohio Dep. Nat. Resour. Water Div. L. Erie Pollut. Surv., Final Rep. 156–170.

Brundin, L. 1951. The relation of O_2 microstratification at the mud surface to the ecology of the profundal bottom fauna. Inst. Freshwater Res. Drottningholm Rep. 32: 32–42.

Burch, J. B. 1972. Biota of freshwater ecosystems. Identification manual no. 3. Freshwater Sphaeracean clams (Mollusca: Pelecypoda) of North America. Water Pollut. Control Res. Ser. 18050 ELDO3/72: 31 p.

Carr, J. F., V. C. Applegate, and M. Keller. 1965. A recent occurrence of thermal stratification and low dissolved oxygen in western Lake Erie. Ohio J. Sci. 65: 319–327.

Carr, J. F., and J. K. Hiltunen. 1965. Changes in the bottom fauna of western Lake Erie from 1930 to 1961. Limnol. Oceanogr. 10: 551–569.

Chandler, D. C. 1964. The St. Lawrence Great Lakes. Verh. Int. Verein. Limnol. 15: 59–75.

Clarke, A. H. 1969. Some aspects of adaptive radiation is recent freshwater molluscs. Malacologia 9: 263.

1973. The freshwater molluscs of the Canadian interior basin. Malacologia 13: 1–509.

Clarke, A. H., and C. O. Berg. 1959. The freshwater mussels of central New York. Mem. Cornell Univ. Agric. Exp. Stn. 361: 1–79.

Clemens, W. A. 1915. Rearing experiments and ecology of Georgian Bay Ephemeridae. Contrib. Can. Biol. 1911–14, Fasc. II. Sess. Pap. 39b: 113–128.

Cook, G. W., P. L. Marciniak, and L. H. Rummel. 1965. Comparative densities of benthic fauna populations in Lake Michigan. U.S. Dep. Health Educ. Welfare, Great Lakes-Ill. River Basins Proj., P.H.S. Region V. Chicago. 25 p. (mimeo.)

Cook, G. W., and R. E. Powers. 1964. The benthic fauna of Lake Michigan as affected by the St. Joseph River. Univ. Mich. Great Lakes Res. Div. Publ. 11: 68–76.

Cook, G. W., and C. Risley. 1963. The distribution of phytoplankton and benthic fauna of Lake Michigan. A preliminary report. U.S. Dep. Health, Educ. Welfare, Great Lakes-Ill. River Basins Proj., P.H.S. Region V. Chicago. 12 p. (mimeo.)

Crocker, D. W., and D. W. Barr. 1968. Handbook of the crayfishes of Ontario. R. Ont. Mus. Misc. Publ. Univ. Toronto Press. 158 p.

Davies, R. W. 1971. A key to the freshwater Hirudinoidea of Canada. J. Fish. Res. Board Can. 28: 543–552.

Eddy, S. 1943. Limnological notes on Lake Superior. Proc. Minn. Acad. Sci. 11: 34–39.

Eggleton, F. E. 1936. The deep water bottom fauna of Lake Michigan. Pap. Mich. Acad. Sci. Arts Lett. 21: 599–612.

1937. Productivity of the profundal benthic zone in Lake Michigan. Pap. Mich. Acad. Sci. Arts Lett. 22: 593–611.

Flint, R. F. 1971. Glacial and Quaternary geology. Wiley and Sons, New York, N.Y. 892 p.

Freitag, R., P. Fung, J. S. Mothersill, and G. K. Prouty. 1973a. Geographical distribution and spatial relationships of benthic macroinvertebrates of Nipigon Bay, Lake Superior, Ontario. Lakehead Univ. MS Rep.: 1–29.

1973b. On the distribution of the benthic fauna of Thunder Bay and northern Lake Superior. Lakehead Univ. MS Rep.: 1–58.

Frey, D. G. 1965. Other invertebrates — an essay in biogeography, p. 613–631. *In* H. E. Wright and D. G. Frey [ed.] The Quaternary of the United States. Princeton Univ. Press, Princeton, N. J. 922 p.

Gannon, J. E. 1972. Aquatic Acari in the Great Lakes. Abstr. 15th Conf. Great Lakes Res. 1972. p 151.

German, M. J. W. 1967. Biological survey of the Kaministikwia River and Thunder Bay, 1965–1966. Ont. Water Resour. Comm. Rep. 1967: 1–24.

1968. Biological survey of Nipigon Bay 1966–1967. Ont. Water Resour. Comm. Rep. 1968: 1–22.

German, M. J. W., and D. M. Pugh. 1969. Biological evaluation of the pollution status of Jackfish Bay, Lake Superior. Ont. Water Resour. Comm. Rep. 1969: 1–17.

Goodrich, C. 1932. The Mollusca of Michigan. Univ. Mich. Mus. Handb. 5: 1–120.

Goodrich, C., and H. van der Schalie. 1932. The Naiad species of the Great Lakes. Occas. Pap. Mus. Zool. Univ. Mich. 233: 1–14.

Hamilton, A. L., O. A. Saether, and D. R. Oliver. 1969. A classification of the Nearctic Chironomidae. J. Fish. Res. Board Can. Tech. Rep. 124: 1–42.

Heard, W. H. 1962. The Sphaeriidae (Mollusca: Pelecypoda) of the North American Great Lakes Am. Midl. Nat. 67: 194–198.

Heard, W. H., and J. B. Burch. 1966. Key to the genera of freshwater pelecypods (mussels and clams) of Michigan. Univ. Mich. Mus. Zool. Circ. 4: 1–14.

Henson, E. B. 1966. A review of Great Lakes benthos research. Univ. Mich. Great Lakes Res. Div. Publ. 14: 37–54.

1970. *Pontoporeia affinis* (Crustacea, Amphipoda) in the Straits of Mackinac region. Proc. 13th Conf. Great Lakes Res. 1970: 601–610.

Herrington, H. B. 1962. A revision of the Sphaeriidae of North America (Mollusca: Pelecypoda). Misc. Publ. Mus. Zool. Univ. Mich. 118: 1–74.

Hesse, R., W. C. Allee, and K. P. Schmidt. 1951. Ecological animal geography. Univ. Chicago Press, Chicago, Ill. 175 p.

Hiltunen, J. K. 1967. Some oligochaetes from Lake Michigan. Trans. Am. Microsc. Soc. 86: 433–454.

1969a. Distribution of oligochaetes in western Lake Erie, 1961. Limnol. Oceanogr. 14: 260–264.

1969b. Invertebrate macrobenthos of western Lake Superior. Mich. Acad. 1: 123–133.

1969c. The benthic macrofauna of Lake Ontario. Great Lakes Fish. Comm. Tech. Rep. No. 14: 39–50.

Holsinger, J. R. 1972. Biota of freshwater ecosystems. Identification manual No. 5. The freshwater amphipod crustaceans (Gammaridae) of North America. Environ. Prot. Agency 18050 ELD.

Hough, J. L. 1962. Geologic framework, p. 3–27. *In* H. J. Pincus [ed.] Great Lakes basin. Am. Assoc. Adv. Sci. Publ. 71.

Howmiller, R. P., and A. M. Beeton. 1970. The oligochaete fauna of Green Bay, Lake Michigan. Proc. 13th Conf. Great Lakes Res. 1970: 15–46.

1971. Biological evaluation of environmental quality, Green Bay, Lake Michigan. J. Water Pollut. Control Fed. 43: 123–133.

Hoy, P. R. 1872. Deep-water fauna of Lake Michigan. Trans. Wis. Acad. Sci. Arts Lett. 1: 98–101.

Jackson, C. T. 1844. Fish and shells from Lake Superior. Proc. Boston Soc. Nat. Hist. 1: 198.

Johnson, M. G., and R. O. Brinkhurst. 1971a. Associations and species diversity in benthic macroinvertebrates of Bay of Quinte and Lake Ontario. J. Fish. Res. Board Can. 28: 1683–1697.

1971b. Production of benthic macroinvertebrates of Bay of Quinte and Lake Ontario. J. Fish. Res. Board Can. 28: 1699–1714.

1971c. Benthic community metabolism in Bay of Quinte and Lake Ontario. J. Fish. Res. Board Can. 28: 1715–1725.

Johnson, M. G., and D. H. Matheson. 1968. Macroinvertebrate communities of the sediments of Hamilton Bay and adjacent Lake Ontario. Limnol. Oceanogr. 13: 99–111.

Jónasson, P. M. 1972. Ecology and production of the profundal benthos in relation to phytoplankton in Lake Esrom. Oikos Suppl. 14: 1–148.

Kenk, R. 1972. Biota of freshwater ecosystems. Identification manual no. 1. Freshwater planarians (Turbellaria) of North America. Environ. Prot. Agency 18050 ELD.

Kew, W. 1888. *Sphaerium corneum* upon the tarsus of *Dytiscus marginalis*. J. Conchol. 5: 363.

Kinney, W. L. 1972. The macrobenthos of Lake Ontario. Proc. 15th Conf. Great Lakes Res. 1972: 53–79.

LaRocque, A. 1953. Catalogue of the recent Mollusca of Canada. Natl. Mus. Can. Bull. 129: 1–406.

1967. Pleistocene Mollusca of Ohio, Pt. 2. Ohio Dep. Nat. Resour., Div. Geol. Surv. Bull. 62: 113–356.

Marshall, A. C. 1939. A qualitative and quantitative study of the Trichoptera of western Lake Erie (as indicated by light-trap material). Ann. Entomol. Soc. Am. 32: 665–688.

Mason, W. T. 1968. An introduction to the identification of chironomid larvae. U.S. Dep. Inter., Fed. Water Pollut. Control Admin., Pollut. Surv. Div. March, 1968: 1–89.

Michaelsen, W. 1900. Oligochaeta. Tierreich 10: 1–575.

Mitropol'skii, V. I., and V. P. Luferov. 1966. Distribution of benthos in the Volga reach of the Rybinsk Reservoir. Inst. Biol. Vnutr. Vod. Acad. Nauk. SSSR. 12: 7–13. (Transl. from Russian by Israel Program for Sci. Transl., Jerusalem, No. 12, 1966)

Mozley, S. C., and L. C. Garcia. 1972. Benthic macrofauna in the coastal zone of southeastern Lake Michigan. Proc. 15th Conf. Great Lakes Res. 1972: 102–116.

Nicholson, H. A. 1873. Contributions to a fauna canadensis; being an account of the animals dredged in Lake Ontario in 1872. Can. J. Sci. Lit. Hist. N. S. 13: 490–506.

Poddubnaya, T. L. 1966. Bottom fauna of the Cheropovets Reservoir in the first two years of its existence. Inst. Biol. Vnutr. Vod. Acad. Nauk SSSR 12: 20–33. (Transl. from Russian by Israel Program for Sci. Transl., Jerusalem, No. 12, 1966)

Powers, C. F., and W. P. Alley. 1967. Some preliminary observations on the depth distribution of macrobenthos in Lake Michigan. Univ. Mich. Great Lakes Res. Div. Rep. 30: 112–125.

Powers, C. F., and A. Robertson. 1968. Subdivisions of the benthic environment of the upper Great Lakes, with emphasis on Lake Michigan. J. Fish. Res. Board Can. 25: 1181–1197.

Rawson, D. S. 1953. The bottom fauna of Great Slave Lake. J. Fish. Res. Board Can. 25: 254–283.

Reighard, J. E. 1894. A biological examination of Lake St. Clair. Bull. Mich. Fish. Comm. No. 4, Append. 11th Bienn. Rep. (1892–4): 60 p.

Ricker, K. E. 1959. The origin of two glacial relict crustaceans in North America, as related to Pleistocene glaciation. Can. J. Zool. 37: 871–893.

Robertson, A. D. 1915. The mollusca of Georgian Bay. Contrib. Can. Biol. 1911–1914, Fasc. II, Sess. Pap. 39b: 95–111.

Robertson, A., and W. P. Alley. 1966. A comparative study of Lake Michigan macrobenthos. Limnol. Oceanogr. 11: 576–583.

Robertson, A., and C. F. Powers. 1967. Comparison of the benthic distribution of organic matter in the five Great Lakes. Univ. Mich. Great Lakes Res. Div. Rep. 30: 1–18.

Sæther, O. A. 1969. Some Nearctic Podomininae, Diamesinae, and Orthocladiinae (Diptera, Chironomidae). Bull. J. Fish. Res. Board Can. 170: 1–154.

1970. Nearctic and Palaearctic *Chaoborus* (Diptera: Chaoboridae). Bull. Fish. Res. Board Can. 174: 1–57.

1973. Taxonomy and ecology of 3 new species of *Monodiamesa* Kieffer, with keys to Nearctic and Palaearctic species of the genus (Diptera: Chironomidae). Bull. Fish. Res. Board Can. 30: 665–679.

Sars, G. O. 1915. Entomostraca of Georgian Bay. Contrib. Can. Biol. 1911–1914, Fasc. II, Sess. Pap. 39b: 221–222.

Sawyer, R. T. 1972. North American freshwater leeches, exclusive of the Piscicolidae, with a key to all species. Ill. Biol. Monogr. 46: 1–154.

Schelske, C. L., and J. C. Roth. 1973. Limnological survey of lakes Michigan, Superior, Huron and Erie. Univ. Mich. Great Lakes Res. Div. Publ. 17: 1–108.

Schneider, J. C., F. F. Hooper, and A. M. Beeton. 1969. The distribution and abundance of benthic fauna in Saginaw Bay, Lake Huron. Proc. 12th Conf. Great Lakes Res. 1969: 80–90.

Schuytema, G. S., and R. E. Powers. 1966. The distribution of benthic fauna in Lake Huron. Univ. Mich. Great Lakes Res. Div. Publ. 15: 155–163.

Segerstråle, S. G. 1962. The migration and prehistory of the glacial relicts of Eurasia and North America. A survey and discussion of modern views. Int. Rev. Gesamten Hydrobiol. 47: 1–25.

Shelford, V. E., and M. W. Boesel. 1942. Bottom animal communities of the island area of western Lake Erie in the summer of 1937. Ohio J. Sci. 42(5): 179–190.

Shrivastava, H. N. 1974. Macrobenthos of Lake Huron. J. Fish. Res. Board Can. Tech. Rep. 449. (In press)

Smith, F. 1919. Lake Superior lumbriculids, including Verrill's *Lumbricus lacustris*. Proc. Biol. Soc. Wash. 32: 33–40.

Smith, S. I. 1874a. The Crustacea of the fresh waters of the United States. Synopsis of the higher freshwater Crustacea of the northern United States. Rep. U.S. Comm. Fish. 1872–73(2): 637–665.

1874b. Sketch of the invertebrate fauna of Lake Superior. Rep. U.S. Comm. Fish 1872–73(2): 690–707.

Smith, S. I., and A. E. Verrill. 1871. Notice of the invertebrate dredged in Lake Superior in 1871, by the U.S. Lake Survey, under the direction of Gen. C. B. Comstock, S.I. Smith, naturalist. Am. J. Sci. 2: 448–454.

Stimpson, W. 1871. On the deep-water fauna of Lake Michigan. Am. Nat. 4: 403–405.

Surber, E. W. 1955. Results of a biological survey of Saginaw Bay, June 24, 1955. Rep. Mich. Water Resour. Comm. 3 p.

Surber, E. W., and H. L. Cooley. 1952. Bottom fauna studies of Green Bay, Wisconsin, in relation to pollution. U.S. Public Health Serv. Comm. Water Pollut. Washington, D.C.

Taylor, D. W. 1965. The study of Pleistocene nonmarine mollusks in North America, p. 597–611. *In* H. E. Wright and D. G. Frey [ed.] The quaternary of the United States. Princeton Univ. Press, Princeton, N.J. 922 p.

Teter, H. E. 1960. The bottom fauna of Lake Huron. Trans. Am. Fish. Soc. 89: 193–197.

Thomas, M. L. H. 1966. Benthos of four Lake Superior bays. Can. Field Nat. 80: 200–212.

Veal, D. M., and D. S. Osmond. 1968. Bottom fauna of the western basin and nearshore Canadian waters of Lake Erie. Proc. 11th Conf. Great Lakes Res., Univ. Mich. Great Lakes Res. Div. Publ. 15: 151–160.

Ward, H. B. 1896. A biological examination of Lake Michigan in the Traverse Bay region. Bull. Mich. Fish. Comm. No. 6: 99 p.

White, H. T. 1915. Bryozoa of the Georgian Bay region. Contrib. Can. Biol. 1911–1914, Fasc. II, Sess. Pap. 39b: 195–199.

Williams, W. D. 1970. A revision of North American epigean species of *Asellus* (Crustacea: Isopoda). Smithson. Contrib. Zool. 49: 1–80.

Wood, K. G. 1963. The bottom fauna of western Lake Erie, 1951–52. Proc. 6th Conf. Great Lakes Res., Univ. Mich. Great Lakes Res. Div. 10: 258–265.

Wright, S. 1955. Limnological survey of western Lake Erie. U.S. Fish Wildl. Serv. Spec. Sci. Rep. Fish. No. 139: 341 p.

Wright, S., and W. M. Tidd. 1933. Summary of limnological investigations in the western end of Lake Erie, 1929–30. Trans. Am. Fish. Soc. 63: 271–285.

Zooplankton of the St. Lawrence Great Lakes — Species Composition, Distribution, and Abundance[1]

N. H. F. WATSON

Great Lakes Biolimnology Laboratory
Canada Centre for Inland Waters, Burlington, Ont. L7R 4A6

WATSON, N. H. F. 1974. Zooplankton of the St. Lawrence Great Lakes — species composition, distribution, and abundance. J. Fish. Res. Board Can. 31: 783–794.

Recent studies of zooplankton of the St. Lawrence Great Lakes have concentrated on a broad synoptic coverage of sampling stations and repeated cruises throughout a growing season. This has resulted in a considerable amount of detail about seasonal changes in species composition, total numbers, and vertical and horizontal distributions. Investigators have treated the data to show differences in distribution over the lakes on a cruise and cruise mean averages for each lake, often weighted by area to provide relative abundance figures over the season and between lakes.

Maximum numbers were observed in Lake Erie (225,000/m^3). Considerably fewer organisms were found in periods of peak abundance in Lake Ontario (55,000/m^3) and Lake Huron (22,000/m^3). No firm estimates are available for Lake Superior but numbers from one cruise (8000/m^3) indicate still lower values there. Biomass estimates (either as ash-free weight of material from planktonnet hauls or from conversions of numbers to biomass from dry weight factors for individual species) are highest for Lake Erie, but reflect the larger size of organisms in the other lakes, especially Huron and Superior.

Species distributions are now reasonably well known for crustaceans, except in one or two taxa of the cladocerans *Daphnia* and *Bosmina* whose variability should be investigated more fully. Recent studies have been made on the rotifers, but their numbers, distribution, and ecological role is not fully defined. Similarly, the distribution and role of protozoan groups have been largely ignored.

Several computer techniques are suggested for the handling and analysis of the large quantities of data generated on lakewide surveys including community coefficients and cluster analyses. More attention should be given to determining sampling intervals to obtain information which can precisely detect changes in abundance from year to year, and better population dynamics and production data are needed to relate zooplankton stocks to eutrophication.

WATSON, N. H. F. 1974. Zooplankton of the St. Lawrence Great Lakes — species composition, distribution, and abundance. J. Fish. Res. Board Can. 31: 783–794.

Les études récentes du zooplancton des Grands lacs laurentiens ont consisté principalement en une couverture synoptique des stations d'échantillonnage et en des campagnes répétées durant une saison de croissance. Il en est résulté une masse de données détaillées sur les changements saisonniers de composition des espèces, des nombres totaux et de leur distribution, tant verticale qu'horizontale. Des chercheurs ont traité ces données de façon à démontrer des différences, au cours d'une campagne ou entre les moyennes des campagnes, pour chaque lac, moyennes souvent pondérées par région en vue de fournir des chiffres sur l'abondance relative au cours d'une saison ou entre les lacs.

On a trouvé des nombres maxima dans le lac Erié (225,000/m:). Des nombres beaucoup moins considérables ont été observés, même en période de pointe, dans le lac Ontario (55,000/m:) et le lac Huron (22,000/m:). Nous n'avons pas d'estimé ferme pour le lac Supérieur, mais les résultats d'une campagne (8000/m:) indiquent des valeurs encore plus basses dans ce lac. Les estimés de biomasse, calculés soit à partir du poids sans les cendres de matériel provenant de traits de filet à plancton, soit par conversion de nombres en biomasse à partir d'indices de poids sec pour des espèces individuelles, accusent un maxi-

---

[1] This paper, part of a special issue that comprises a comprehensive review of Limnology in Canada, was prepared to mark the 19th Congress of the International Association of Limnology (SIL), in Winnipeg, Man., during August 1974.

Printed in Canada (J3263)

mum dans le lac Erié, mais reflètent la plus grande taille des organismes dans les autres lacs, surtout les lacs Huron et Supérieur.

On connaît assez bien la distribution des espèces de crustacés, sauf pour un ou deux taxa des cladocères *Daphnia* et *Bosmina*, dont la variabilité devrait être étudiée davantage. On a fait des études récentes sur les rotifères, mais on n'a pas entièrement défini leurs nombres, distribution et rôle écologique. De la même façon, on a ignoré en grande partie la distribution et le rôle des groupes de protozoaires.

Nous suggérons plusieurs techniques d'ordinateur pour la manipulation et l'analyse de la masse de données recueillies au cours de recensements à la grandeur des lacs, y compris coefficients de communautés et analyses de groupements. On devrait décider avec plus de soin des intervalles d'échantillonnage en vue de détecter avec plus de précision les variations d'abondance d'une année à l'autre. On a besoin de meilleures données sur la dynamique des populations et la production, afin de pouvoir établir la relation entre les stocks de zooplancton et l'eutrophisation.

Accepted October 31, 1973

Davis (1966) summarized the state of knowledge of the plankton of the Great Lakes, underscoring the need for quantitative seasonal studies of phytoplankton and zooplankton and the need to relate their abundance with the unique physical, chemical, and biotic environment in the lakes. Several studies in the intervening years have provided partial answers to some of these questions, but have in turn raised others perhaps equally fundamental.

Since 1966 there has been extensive synoptic sampling of four of the lakes at least once each year: in Lake Ontario 1967–72, in Lake Erie 1968–72, in Lake Huron (exclusive of Georgian Bay) 1971–72, and in Lake Superior 1971 and 1973, as part of the monitoring program of the Canada Centre for Inland Waters. In addition, Lake Ontario was subjected to several intensive programs by agencies of the Canadian and U.S. federal governments, provincial and state agencies, and university groups during the International Field Year for the Great Lakes (IFYGL), from March 1972 to June 1973. Zooplankton collections were made at many of the stations visited, along with samples for phytoplankton species composition, surface chlorophyll *a* concentration, and a series of chemical and physical determinations. Individual studies of plankton communities of the lakes were also made by other agencies and investigators. The published studies of the plankton communities of Parry Sound (Carter 1969), of transects along Lake Erie (Davis 1968, 1969), of Lake Michigan (Gannon 1972; Wells 1969), and of Lake St. Clair (Leach 1973) fill important gaps in knowledge of the regional distribution of zooplankton in the lakes.

Although much of the information from this sampling has not been fully analyzed, a considerable amount of material is available describing seasonal changes in species composition and abundance of crustacean zooplankton in the lakes. Patalas (1969, 1972) described the abundance and distribution of plankton of Lake Ontario in the summer of 1967 and the lake-wide abundance of plankton of lakes Ontario, Erie, Huron, and Superior in August 1968. He considered summer to be the period of maximum abundance and species richness, and related total zooplankton abundance in the top 50 m to surface chlorophyll concentrations and heat content in surface waters. More recently Watson and Carpenter (1974) described seasonal changes in species composition and plankton net biomass of lakes Ontario and Erie, based on 1970 sampling, and of Lake Huron based on 1971 collections.

Other authors have tackled the questions of apparent changes in species composition and abundance in the lakes, particularly lakes Erie and Michigan, using existing records, those for Lake Erie going back to 1940. Brooks (1969), Gannon and Beeton (1971), and Wells (1970), refer to changes in abundance and species composition of plankton in the Great Lakes, especially lakes Erie and Michigan, and relate these changes to changes in level of eutrophication and to selective predation pressure in the lakes. Patalas (1972) relates crustacean zooplankton abundance to heat content and level of eutrophication in the lakes.

The purpose of this paper is to add to what was previously known of the species composition of zooplankton in each of the lakes and to demonstrate seasonal changes in abundance. This information will then be used to evaluate factors which have been considered important in zooplankton species composition and abundance. Current trends in zooplankton research on the Great Lakes will also be assessed.

Species Composition

As Patalas (1972) pointed out, at least 15 species of copepods and cladocerans are known to be common to at least four of the Great Lakes. Studies by Wells (1960, 1970) and Gannon (1972) indicate these species are present in Lake Michigan as well.

Collections from 1971 (N. H. F. Watson unpublished data) add *Diaptomus siciloides* Lillj. and *Eubosomina coregoni* Baird to the species list for Lake Superior, and McNaught and Buzzard (1973) report *Diatomus ashlandi* from Lake Ontario. It seems that this list of 15 can be expanded to include almost all the 30 or so species of crustaceans listed in Table 1. Other littoral and a few rarer forms can also be expected to be found in each of the Great Lakes. Abundance and time of occurrence of each species varies greatly from lake to lake, however.

Limnocalanus macrurus is a characteristic inhabitant of the colder deep waters of all the main lakes. Leach (1973) considers that individuals in Lake St. Clair are passive migrants from Lake Huron and some individuals found in the Western Basin of Lake Erie (Watson et al. 1973) may come from the same source. Gannon and Beeton (1971) cite evidence that abundance and distribution declined in Lake Erie since 1929–30, when the species was noted at many stations while water temperatures were low. Recent occurrences of anoxic conditions in the Central Basin and oxygen depletions in the Eastern Basin, as well as intensive predation by planktiverous fish, are regarded as factors in the decline of the species. However, there is evidence of recolonization of the Western Basin by this and other species of calanoids via flows from southern Lake Huron, at least during winter and early spring (Jahoda *1948;* Watson et al. 1973).

Eurytemora affinis was first recorded from the plankton of Lake Ontario by Anderson and Clayton (1959) as *Eurytemora* sp., and has subsequently been recorded in all the other lakes (Engel 1962; Faber and Jermolajev 1966; Patalas 1972; Robertson 1966) and in dune ponds along the eastern shore of Georgian Bay (Carter 1971). It is obviously now widespread in the Great Lakes and in some areas may be important as food for planktivorous fish, over and above its apparent abundance in the plankton (Faber and Jermolajev 1966). The species has either spread rapidly through the system or has increased in numbers considerably in the past one or two decades, or possibly has done both.

Diacyclops bicuspidatus thomasi is the most abundant cyclopoid in all the lakes. In parts of lakes Erie and Ontario, copepodites of this form

TABLE 1. Crustacean zooplankton species recorded from the Great Lakes; list modified from Patalas 1972.

Species	Lake Superior	Lake Mich.[a]	Lake Huron	Lake St. Clair[b]	Lake Erie	Lake Ont.
Senecella calanoides Juday	*	*	*[c]			*
Limnocalanus macrurus Sars	*	*	*	*	*	*
Eurytemora affinis (Poppe)	*	*	*	*	*	*
Epischura lacustris Forbes	*	*	*	*	*	*
Diaptomus sicilis Forbes	*	*	*	*	*	*
D. ashlandi Marsh	*	*	*	*	*	*[c]
D. minutus Lillj.	*	*	*	*	*	*
D. oregonensis Lillj.	*	*	*	*	*	*
D. siciloides Lillj.	*	*	*	*	*	*
D. pallidus Hennrick				*	*	*
Diacyclops bicuspidatus thomasi Forbes	*	*	*	*	*	*
Acanthocyclops vernalis Fischer	*	*	*	*	*	*
Mesocyclops edax (Forbes)	*	*	*	*	*	*
Tropocyclops prasinus mexicanus Keifer		*	*	*	*	*
Osphranticum labronectum Forbes		*				
Alona spp.		*	*[c]	*	*	*
Bosmina longirostris O.F.M.	*	*	*	*	*	*
Ceriodaphnia lacustris Birge		*	*	*	*	*
Chydorus sphaericus O.F.M.		*	*	*	*	*
Daphnia ambigua Scour.					*	
D. galeata mendotae Birge	*	*	*	*	*	*
D. longiremis Sars		*		*		
D. parvula Fordyce		*		*		
D. pulex DeGeer				*		
D. retrocurva Forbes	*	*	*	*	*	*

[a] Gannon (1972).
[b] Leach (1973).
[c] Watson and Carpenter (1974).

may occasionally be the most abundant zooplankter. Nauwerck et al. (1972) found no evidence of an arrested development of this species in Lake Ontario, and Watson et al. (1973) considered the accumulation and sudden disappearance of copepodite forms in all three basins of Lake Erie to be circumstantial evidence of arrested development as copepodite IV stage, similar to the situation in inland lakes in Wisconsin (Birge and Juday 1908).

As Gannon (1972) and Patalas (1972) point out, the bulk of cladoceran fauna of the Great Lakes is largely confined in space to inshore and surface waters and in time to the summer months.

There are major difficulties in the specific identification of several taxa of cladocerans which possess a wide range of phenotypic variability, only some of which is attributable to cyclomorphosis. Brooks (1957) has contributed to the description and taxonomy of the *Daphnia* group. Discrepancies between past studies and current usage are pointed out by Davis (1966) who noted that two surveys of Lake Erie in the early 1930s disagreed markedly in their interpretation of the dominant form in the lake, one group mentioning only *D. retrocurva* and the other *D. pulex*. Although the taxonomy is now considered stable enough to define dominant forms, practical difficulties exist in identification of a considerable proportion of the large populations in inshore areas. Comparisons with past species compositions must be conjectural at best.

Similar problems exist within the family *Bosminidae*, in which Deevey and Deevey (1971) have recently recognized *Eubosmina* Seligo as a separate genus for forms similar to the nonmucronate *Eubosmina coregoni* (Baird). Patalas (1972) points out that there is confusion over the form within this group that Deevey and Deevey (1971) considered an indicator of oligotrophic conditions; it is not the nonmucronate *E. coregoni* nor is it likely to be the mucronate form of *Eubosmina* found by Nauwerck et al. (1972) in Lake Ontario, and by Watson et al. (1973) in Lake Erie, which comes closest in description to *E. longispina* (Leydig) according to Deevey and Deevey (1971). Clearly, both taxonomic distinctions and ecological tolerances of the several forms in the lakes, including those variants lumped under *Bosmina longirostris*, must be worked out before changes in species composition and their roles as indicators of water quality can be documented and interpreted.

Mysis relicta (Lovén) has been reported as a semiplanktonic element of the fauna of all the lakes by various authors. Its seasonal abundance and horizontal distribution in the lakes excluding Lake Michigan and Georgian Bay are described by Carpenter et al. (1974). The proportion of animals present on the bottom at any time is not known, although studies of the vertical distribution have been made (Beeton 1960; Foulds 1972). Its abundance is limited to areas deeper than 25 m. All these studies indicate that much of the population remains in the water column in the very deep waters of the lakes during daylight hours.

The study of species composition and abundance of rotifers and protozoa in plankton of the Great Lakes has progressed little since 1966, when Davis reviewed existing surveys. Davis (1968, 1969) and Leach (1973) described the protozoa and rotifers of Lake Erie and Lake St. Clair, and Nauwerck (1972) described seasonal changes in rotifer fauna from three stations in Lake Ontario, with notes on the lakes other than Lake Michigan. Davis (1969) noted 15 taxa of rotifers mostly of genera in Lake Erie in October 1967, and Leach (1973) identified 24 taxa of rotifers in Lake St. Clair. Nauwerck (1972), in probably the most thorough and up to date taxonomic study, recognized close to 50 taxa in lakes Erie and Ontario, 30 in Lake Huron, and 20 in Lake Superior (Table 2). He found close affinities between species compositions of lakes Ontario and Erie and the Saginaw Bay region of Lake Huron.

Seasonal Abundance of Zooplankton

Only a few recent studies on the plankton of the lakes provide estimates of the changes in populations or biomass on a seasonal or year-round basis. Watson and Carpenter (1974) compared the relative abundance of major species of crustaceans in lakes Ontario, Erie, and Huron from monthly cruises over much of the year. Gannon (1972) described crustacean zooplankton abundance in Green Bay in Lake Michigan (off Milwaukee) and from surface samples collected from the Milwaukee, Wisconsin – Luddington, Michigan ferry. No comparable studies have been published yet for Lake Superior, although six sets of samples were obtained from May to December 1973.

The general pattern of crustacean zooplankton concentrations (numbers/m^3) in the three lakes is of low winter numbers (largely calanoid copepods), a rapid spring rise to peak concentrations during the summer or late summer, and a rapid decline to winter numbers late in the season (Fig. 1). Timing and height of the maximum varies from lake to lake, associated with different species composition and conditions in each lake. Maximum values for Lake Erie were reached in early June, although peak values in the Western Basin did not occur until August. Maximum concentrations of zooplankton were also found in lakes Ontario and Huron in August.

TABLE 2. Common rotifer species of the Great Lakes compiled from samples collected by personnel of the Canada Centre for Inland Waters and based on identifications made by Dr A. Nauwerck on species from lakes Ontario and Erie, 1970. Lake St. Clair records are from Leach (1973).

Species	Lake Ontario	Lake Erie	Lake St. Clair	Lake Huron	Lake Superior
Asplanchna sp.		*		*	*
A. priodonta Gosse	*		*		
Brachionus sp.		*		*	*
B. angularis (Plate)	*		*		
B. calcyiflorus Pallas	*		*		
Chromogaster ovalis (Bergendal)			*		
Collotheca mutabilis Hudson	*		*		
Conochiloides sp.			*		
Conochilus sp.			*		
C. unicornis Rousselet	*	*	*		*
Euchlanis dilatata Ehrenberg			*		
Filinia sp.		*		*	*
F. longiseta (Ehrenberg)	*		*		
Gastropus sp.					*
G. stylifer Imhof			*		
Kellicottia longispina (Kellicott)	*	*	*	*	*
K. bostoniensis (Rousselet)		*		*	
Keratella cochlearis Ahlstrom	*	*	*	*	*
K. cochlearis v. *robusta* (Lauterb.)	*				
K. cochlearis v. *hispida* (Lauterb.)	*				
K. crassa Ahlstrom	*	*		*	
K. earlinae Ahlstrom	*	*			
K. hiemalis Carlin	*	*		*	
K. quadrata (O.F.M.)	*	*	*	*	*
K. quadrata v. *canadensis* Berzins	*	*			
K. taurocephala Ahlstrom		*			
K. valga Ahlstrom[a]			*		
Lecane sp.			*		
Lepadella sp.		*	*		
Notholca sp.		*	*		
N. acuminata Hudson and Gosse	*	*		*	*
N. foliacea (Ehrenberg)		*			
N. squamula (O.F.M.)	*	*		*	*
N. striata (O.F.M.)	*	*		*	
Ploesoma hudsoni (Imhof)	*			*	
P. truncatum (Levander)	*		*		
Polyarthra sp.		*	*		*
P. dolichoptera Idelson	*				
P. major Burckhardt	*	*		*	*
P. remata Skorikov	*				
P. vulgaris Carlin	*	*	*	*	
Synchaeta sp.		*	*	*	*
S. lackowitziana Lucks	*				
S. pectinata Ehrnb.	*	*		*	
S. stylata Wierzejski	*				
Trichocerca cylindrica (Imhof)	*		*		
T. multicrinis (Kellicott)	*	*	*	*	
T. porcellus (Gosse)	*				
Trichotria tetractis (Ehrenberg)			*		

[a] Nauwerck sees *K. valga* as a variety of *K. hiemalis*.

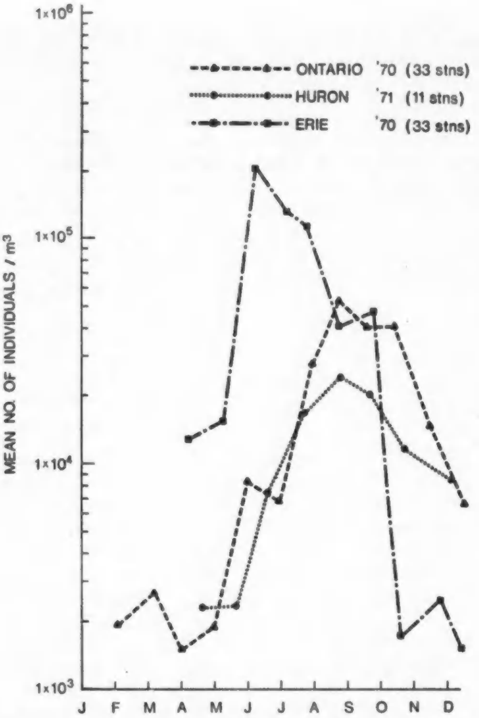


FIG. 1. Seasonal abundance of crustacean zooplankton in lakes Ontario, Erie, and Huron.

The range of variation from minimum to maximum average concentrations per cruise was least in Lake Huron (2,000–24,000/m^3), intermediate in Lake Ontario (2,000–55,000/m^3), and greatest in Lake Erie (2,000–200,000/m^3).

Monthly concentrations of total crustaceans cited by Gannon (1972) at the station off Milwaukee Harbor followed a similar pattern to those for lakes Ontario and Huron. However, absolute values per m^3 were considerably less than for the lake averages for these two lakes. Values for a single cruise in Lake Superior (8000/m^3) were considerably less than those for the other three lakes and indicate either a slower development rate of plankton or a considerably smaller seasonal standing crop.

The zooplankton found in the Great Lakes can be arranged in a sequence from the relatively sparse, calanoid-dominated plankton of the open waters of Lake Superior, through Lake Huron with somewhat higher standing stocks, to the faunas of lakes Ontario and Michigan where calanoids dominate year-round in the deep waters, and large numbers of cyclopoids and cladocerans occur at the surface, especially in summer. The final step in this evolution is found over much of Lake Erie and in shallow areas of the other lakes, where deepwater calanoids are found in numbers only in the winter months and cyclopoids and cladocerans predominate year-round, often in high numbers. Patalas (1972) indicates that his proposed general relation to explain zooplankton abundance in terms of chlorophyll *a* concentration does not hold well in lakes Erie and Ontario. Also, the proportions of calanoids to cyclopoids and cladocera, suggested by Gannon (1972) as an indication of trophic status of the lakes, seems to reflect only changes in the relative abundance of the latter groups. Minimal values of zooplankton of about 2000/m^3 in each of lakes Erie, Ontario, and Huron cited by Watson and Carpenter (1974) are largely made up of calanoids in each case. Apparently increasing eutrophication allows development of larger summer populations of cyclopoids and cladocerans, whereas populations of calanoids remain roughly the same or became slightly diminished.

All studies on seasonal distribution published to date are for periods of 1 yr or less. Long-term synoptic records in excess of 1 yr are scarce, so it is unclear how much year-to-year variation results from climatic variability. Gannon (1972) reported differences of 50% in total abundance on sampling dates a year apart, as well as considerable differences in species composition of the catch.

Horizontal Distribution Patterns

There is considerable variation in abundance of crustacean zooplankton over the surface of each lake. This is true when numbers in a net haul are expressed either in terms of abundance (per m^2) under a unit area (Patalas 1969, 1972), or in terms of concentration (per m^3) in the water column (Watson and Carpenter 1974).

Numbers per m^3 are generally highest inshore or in shallow areas like the Western Basin of Lake Erie or the Saginaw Bay region of Lake Huron. Patalas (1969) considers that differences in overall abundance in the water column will be less pronounced than differences in overall concentration. Even so, his published distribution showed real differences in both total numbers and species composition between inshore and offshore stations. Most cladocerans tend to be more abundant inshore, and many large calanoids are more abundant offshore. The same pattern of differences between inshore and offshore species composition and concentrations was documented in detail for Lake

Ontario by Nauwerck et al. (1972). Of the 37 stations in this study, roughly half were less than 30 m in depth and represented approximately only 20% of the lake area. Average concentrations of cladocerans and cyclopoids were less at the offshore stations year-round, whereas concentrations of calanoids were almost the same as at the inshore stations. Nauwerck also noted that some species (like *Eurytemora affinis*) were restricted to inshore waters, and others (like *Diaptomus minutus*) were excluded from shallower waters. Differences between nearshore and offshore areas are not as marked in Lake Erie, but considerable differences exist in the species composition and abundance at any time between the three major basins of the lake (Watson et al. 1973).

Besides inshore, offshore, and basin differences, large-scale differences in abundance occur within what would appear to be a homogeneous water body. These frequently appear as north-to-south gradients of abundance on lakes Ontario and Erie (Patalas 1969; Nauwerck et al. 1972; Watson et al. 1973). Other patterns will undoubtedly appear when further analysis is performed on lakes Huron and Superior.

These patterns vary with the species composition of the plankton and with time, and may, as Patalas (1969, 1972) points out, be the result of relative movement of the plankton in the lake aided by currents, upwellings, etc. Certainly there appears to a considerable concentration of Western Basin zooplankton forms along the south shore of the Central Basin of Lake Erie associated with water flow patterns.

The movement of zooplankton over long distances must be a complex affair, especially as the organisms may migrate vertically from a water mass moving in one direction into one moving in a different direction (Patalas 1972). However, such processes may not be very strong in the open lake region as they should tend to minimize rather than create population differences between water masses.

Munawar and Nauwerck (1971) described highly variable patterns in abundance of phytoplankton in the surface waters of Lake Ontario, and it would appear essential to perform a station-by-station analysis of abundance of phytoplankton and zooplankton groups to explain the distribution of both. This sort of interaction of phytoplankton and zooplankton, including selective grazing, has been recently suggested by Gliwicz (1969), Porter (1973), and others.

Factors which must affect horizontal distribution as well as abundance of zooplankton are differences in the timing and pattern of life cycles of individual zooplankton species. For example, Watson et al. (1973) indicated at least two spring and summer generations of *Diacyclops bicuspidatus thomasi* in many parts of the Western and Central basins of Lake Erie, with a sudden decline to low values by July, and Nauwerck et al. (1972) reported several generations of the species building up to a maximum abundance in late August in Lake Ontario. In Lake Erie, certain species like *D. bicuspidatus thomasi* reach maximum concentrations first in the Central, then in the Western, and finally in the Eastern Basin. *Daphnia longiremis* reaches maximum numbers first in the Eastern Basin, whereas *D. retrocurva* reaches maximum values first in the Western Basin. The semiplanktonic *Mysis relicta* may have one breeding period per year in Lake Superior and two in lakes Ontario and Huron (Carpenter et al. 1974). Similar differences in life-cycle timing and generation time related to conditions in the lakes probably exist for other species, but await future investigation and analysis.

Vertical Distribution and Vertical Migration

Most sampling of Great Lakes zooplankton has been carried out by vertical net hauls with simple conical nets from a standard depth (50 and 100 m) to the surface. Such sampling integrates the water column through which the net travels but does not delineate the stratum in which the organisms are living. Wells (1960) studied the vertical distribution and migration of zooplankton in Lake Michigan and demonstrated considerable vertical migration for most species. Patalas (1969) reported that 90% of the crustacean zooplankton in the top 100 m of Lake Ontario were in the top 50 m in September, when stratification was at a maximum. When averaged over a 24-h period, he considered that only *Limnocalanus macrurus* and *Diaptomus sicilis* were numerically underrepresented in the top 50 m. Nauwerck et al. (1972) found considerable differences in abundance of many zooplankters from day and night tows from 50 m in the lake and considered that as much as 30% of the total crustacean population moved below 50 m in the day.

An extensive study of vertical migration of Lake Ontario zooplankters was performed throughout the year by Wilson and Roff (1973) and is being related to nutrient regeneration. This study indicated that generally more crustaceans were found below 50 m during the day than suggested by Patalas (1969) especially during parts of the year when cladocerans were less abundant. The largest forms, *Mysis relicta*, *Limnocalanus macrurus*, and *Diaptomus sicilis*, tended to be found deeper than smaller forms, and thus the depth distribution of biomass was considerably different than that for numbers.

D. C. McNaught, (State University of New York, Albany, personal communication) studied the vertical distribution of zooplankton on synoptic cruises of Lake Ontario in 1972–73. He utilized multiple-range sonar techniques to locate and estimate abundance and biomass of crustacean zooplankton. If the technique proves capable of quantification, it will provide a useful approach to the study of particle distribution in the Great Lakes, where extensive vertical migration, changes in horizontal distribution, and changes in seasonal abundance take place.

Biomass Estimates

The first estimates of zooplankton biomass on lakes Ontario, Erie, and Huron were presented by Watson and Carpenter (1974). Two methods were used. Portions of the net hauls were preserved on glass-fiber filters. From these samples dry weights and ash-free dry weights were determined. Also, counts were converted to biomass using the biomass estimates of Wilson and Roff (1973). Concentrations of plankton net (64 μ) chlorophyll *a* were also determined, to measure relative net phytoplankton biomass. Calculated crustacean biomass frequently approximated total plankton net biomass, except when plankton net chlorophyll *a* was high (Fig. 2).

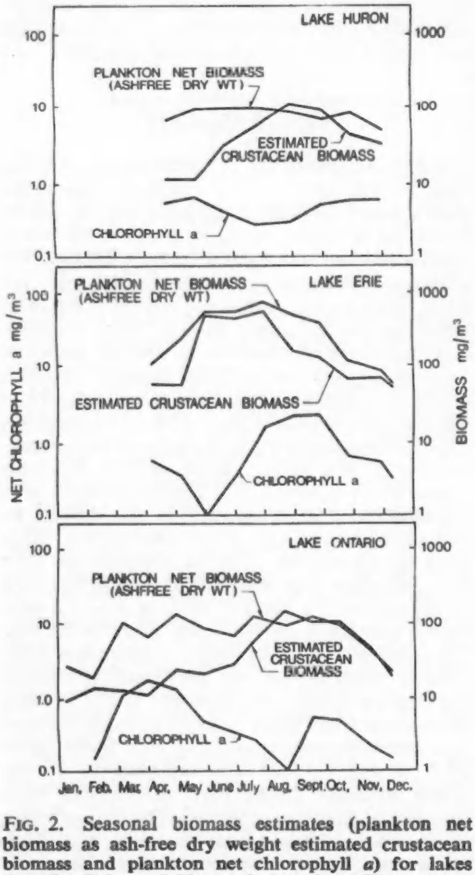


FIG. 2. Seasonal biomass estimates (plankton net biomass as ash-free dry weight estimated crustacean biomass and plankton net chlorophyll *a*) for lakes Ontario, Erie, and Huron (values from Watson and Carpenter 1974).

Plankton net biomass ranged from 80 to 900 mg/m³ per cruise in Lake Erie, 20 to 110 mg/m³ in Lake Ontario, and 70 to 90 mg/m³ in Lake Huron. Generally, there was less variation, both seasonally within lakes and also between lakes, when concentrations were expressed as biomass rather than as numbers of individuals.

When these rather crude biomass values are divided by numbers, the resulting estimates of biomass per individual show similar trends with season in each lake, and differences between lakes (Fig. 3). First there is a tendency for average biomass per individual to decrease from maximum winter values to minima late in the fall. This pattern is clearest in Lake Huron but is also evident in Lake Ontario and is true for Lake Erie from June to December.

Variation in average weight is least in Lake Huron where weight is greatest over the year. Variation is greatest in Lake Ontario, where individuals are lightest over much of the year. This latter finding contradicts the hypothesis of Brooks (1969), Gliwicz (1969), and others, that as trophic state increases size decreases. A similar trend is

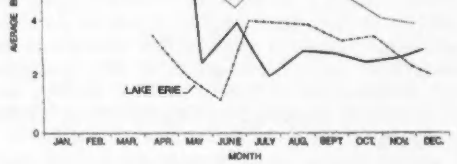


FIG. 3. Seasonal changes in average biomass per individual of the crustacean zooplankton of lakes Ontario, Erie, and Huron.

expected to hold for Lake Superior, where the proportion of large calanoid copepods is considerably greater than in the lower lakes in the few samples examined to date (N. H. F. Watson unpublished data).

When biomass estimates of zooplankton from counts and individual dry weights are compared with those for phytoplankton from cell volumes (Munawar and Nauwerck 1971) at comparable stations in Lake Ontario 1970, standing stocks of zooplankton biomass are 10–20% of those for phytoplankton (assuming a dry weight of phytoplankton of 10% of fresh cell volume). Comparisons from the other lakes are not currently available, but it is expected that in the upper lakes with populations of large, long-lived calanoid copepods, instances when zooplankton biomass will exceed phytoplankton biomass will be common.

Long-term Changes in Zooplankton Populations

Zooplankton abundance figures vary considerably throughout the year and marked horizontal variation exists across each of the lakes at any one time, due in part apparently to rather poorly defined water-mass movements. Therefore, considerable year-to-year variation in total numbers and species composition of zooplankton is to be expected when particular stations or areas are examined. All studies on seasonal distribution published so far are for periods of 1 yr or less, so it is unclear how much year-to-year variation exists and how much results from climatic variability. Gannon (1972) showed differences of 50% in total abundance on sampling dates a year apart as well as considerable differences in species composition of the catch.

Nevertheless, several authors (Bradshaw 1964; Gannon and Beeton 1971; McNaught and Buzzard 1973; others) have attempted to compare zooplankton numbers from several surveys conducted at different times. Quantitative records exist at about 10-yr intervals at stations in the Western Basin of Lake Erie, especially in the Bass Islands region. Samples were collected in different ways on different surveys. Estimates from studies prior to 1960 are averaged values of three or more Juday trap samples taken at different levels in the water column. More recent samples (Davis 1968, 1969; Watson et al. 1973) were collected by vertical hauls of a net whose mouth was lowered to within 2 m of the bottom.

It is difficult to compare abundance figures from each sampling period without estimates of the reliability of the numbers. Hubschman (1960) points out that values of cladoceran abundance obtained from one station on successive days could fluctuate by a factor of 5×.

Most other sampling programs were based on single samples taken weekly or monthly over the same period. The most that can be said is that average values for total crustacean abundance over the period 1940–70, taken at a comparable station in the Bass Island region of Lake Erie by methods not entirely comparable, show some tendency to increase. This increase is in numbers of cladocerans, although maximum station values in 1970 are only slightly higher than those found by Hubschman (1960) in 1959.

Others authors (Brooks 1969; Wells 1970; Gannon and Beeton 1971) have attempted to demonstrate changes in plankton populations in the Great Lakes and relate these to cultural eutrophication. They consider that in more eutrophic situations predation pressure on larger zooplankton by planktiverous fish causes a reduction in size of the plankton present. Brooks (1969) cited evidence that the most important *Daphnia* species in the lake in 1930 was *D. pulex* but recent studies refer to *D. retrocurva*. Davis (1962, 1966) pointed out difficulties with *Daphnia* taxonomy, which probably gave rise to the early records of *D. pulex* in the lake. Wells (1970), in comparing zooplankton species composition in Lake Michigan between 1954 and 1968, found changes in abundance of some species and changes in average size of others. He attributed these changes to the predation pressure of alewives, especially as short-term changes in abundance were also evident between 1966 and 1968. This interpretation assumes that zooplankton reproduction rates do not undergo changes in response to predation pressure. Any relation between predation pressure and changes in zooplankton should deal with production rather than standing stock. This is pointed out by Faber and Jermalejov's (1966) comments on the more frequent occurrence of *Eurytemora affinis* in fish stomachs than in plankton hauls. Despite its relatively large size and apparent selection by fish, this form has been recorded from all the Great Lakes within 15 yr of its first records in the lakes.

In contrast to Brooks, Gliwicz (1969) considers that zooplankters are smaller in more eutrophic waters because bacteria and smaller particles are more available as food items. Smaller organisms apparently prey more effectively on these items. The preliminary figures in this paper do not substantiate a smaller average size zooplankton in Lake Erie, the lake which by morphometry and nutrient loadings is generally agreed to be most eutrophic of the St. Lawrence Great Lakes (Patalas 1972).

Studies on the food of *Limnocalanus macrurus*, one of the larger zooplankters in the lakes, indicate food in the lake in the range 4–24 μ in diameter

(Rigler 1972). Burns (1968) found that *Bosmina longirostris* of less than 1 mm would ingest plastic spheres in the same size range. Therefore, an analysis of the standing crop of food particles alone will not necessarily determine food availability for a range of filter-feeding zooplankters.

Conclusions

Apparently studies of zooplankton of the Great Lakes are still largely in a descriptive phase: species of crustaceans present in the open waters have been well defined. Except in the highly plastic cladocerans, taxonomy is workable and stable and seasonal abundance patterns and a basic pattern of diurnal migration are emerging. However, the smaller forms — rotifers, and especially protozoans — have not been thoroughly examined taxonomically and are either not sampled quantitatively or are ignored by most investigators. Nauwerck (1972) indicates that relatively high numbers of rotifers may be present in all the lakes.

Future studies of interactions of zooplankton, phytoplankton, and fish will depend on accurate estimates of population dynamics and productivity. Such estimates are presently limited by the extent and frequency of the sampling and analysis procedures necessary to accurately measure standing crop and to express such data as production units. Surveys currently being carried out on a monthly basis will, however, provide the basis for an estimate of seasonal changes in stock and an initial estimate of life cycle information for some long-lived species.

New techniques for the design of sampling patterns and methods of analysis now becoming available should produce better estimates of standing stock community structure. Carpenter (1974) and Watson et al. (1974) suggest a direct method for estimating total biomass and phytoplankton biomass by measuring, in weight units, biomass from a plankton net haul and from an integrated water sample. A biomass estimate independent of species abundance figures would appear necessary to describe some of the biological aspects of water quality.

The rather diverse fauna of zooplankton organisms geographically widespread in all the lakes (at least in the case of the crustaceans), whose numbers in any one area change in response to season, shifting water masses, and predation pressure, make it difficult to isolate indicator organisms sensitive enough to the range of conditions in the lakes to be valuable as water quality indicators. Techniques are being developed, however, which it is hoped will enable investigators to consolidate the large masses of data that are relatively easy to collect but difficult to analyze precisely. Most of these techniques involve the use of computers and utilize multivariate regression and cluster analysis procedures. One technique based on the cluster analysis methods employed by Lance and Williams (1966) and Stephenson et al. (1972) is being developed using data reported by Watson and Carpenter (1974). Although results are still being evaluated, it appears that station cluster analyses, using species abundance data and one or more of the indices of similarity suggested by Lance and Williams (1966), provide a sensitive independent measure of homogeneous areas with the lake and of affinities in zooplankton community structure. One index of similarity, a quantitative formulation of a community coefficient developed by Stephenson et al. (1972), was sorted using several strategies depending on the coefficient of correlation, Euclidean distance, nearest neighbor analysis, furthest neighbor analysis, and centroid sorting. Station arrays produced by each of these alternatives are being evaluated. Some of the groupings of stations generated by these methods appear to provide considerable insight into interactions of zooplankton populations. For example, in Lake Erie the four most closely related stations lie within the Central Basin, considered by Burns and Ross (1972) to be the area most likely to develop anaerobic conditions even at times of the year when lake-average oxygen content is high. Among other groupings, some relate stations from sublittoral zones at widely separated geographical areas and others show marked differences in stations which are geographically closely spaced, thus indicating the need for a more tightly spaced sampling pattern in these diverse areas. An extension of this type of analysis allows the objective delineation of species groups and the selection of sensitive indicator–species combinations for relation to water quality conditions. Such techniques, coupled with design analyses of the type outlined by Frontier (1973), should allow development of sampling patterns yielding maximum information about community structure, patchiness, and movements of zooplankton in the lakes.

Once this advanced descriptive phase of community analysis is completed, it should be possible to develop production estimates from selected areas in the Great Lakes in conjunction with production and standing crop estimates of other components of the food web; this should lead to better understanding of the effects of cultural eutrophication and of the introduction of toxic materials into the lakes by extensive human activities in the watershed.

Acknowledgments

This paper has drawn heavily on currently unpublished data files at the Canada Centre for Inland Waters and compilations of information from the Institute for Environmental Science and Engineering (formerly Great Lakes Institute), University of Toronto, as well as considerable discussions with colleagues working on problems of specific geographic areas in the Great Lakes region, most notably Drs A. Nauwerck, J. E. Gannon, R. R. Langford, J. M. Leach, D. S. McNaught, and Mr G. F. Carpenter. Dr R. A. Vollenweider initiated many of the studies carried out by C.C.I.W. and Mr E. E. Pickett has been involved with the analyses of the community structure. Mrs L. Devey and Mr B. Wilson helped with preparation of the manuscript.

Anderson, D. V., and D. Clayton. 1959. Plankton in Lake Ontario. Ont. Dep. Lands For., Maple, Ont. Res. Div. Phys. Res. Note I: 2 p. (mimeo.)

Beeton, A. M. 1960. The vertical migration of *Mysis relicta* in lakes Huron and Michigan. J. Fish. Res. Board Can 17: 512–539.

1969. Changes in the environment and biota of the Great Lakes, p. 150–187. *In* Eutrophication: causes, consequences, correctives. Nat. Acad. Sci., Washington, D.C.

Birge, E. A., and C. Juday. 1908. A summer resting stage in the development of *Cyclops bicuspidatus* Claus. Trans. Wis. Acad. Sci. Arts Lett. 16: 1–9.

Bradshaw, A. S. 1964. The crustacean zooplankton picture; Lake Erie 1939–49–59; Cayuga 1910, 1951–61. Verh. Int. Verein. Limnol. 15: 700–708.

Brooks, J. L. 1957. The systematics of North American *Daphnia*. Mem. Conn. Acad. Arts Sci. 13: 1–180.

1969. Eutrophication and changes in the composition of the Great Lakes, p. 236–255. *In* Eutrophication: causes, consequences, correctives. Nat. Acad. Sci., Washington, D.C.

Burns, C. W. 1968. The relationship between body size of filter feeding Cladocera and the maximum size of particle ingested. Limnol. Oceanogr. 13: 675–678.

Burns, N. M., and C. Ross. 1972. Project Hypo — an intensive study of the Lake Erie Central Basin hypolimnion and related surface water phenomena. Can. Cent. Inland Waters Pap. 6: 1–182.

Carpenter, G. F. 1974. A proposed method suitable for the monitoring of biomass in lakes. J. Fish. Res. Board Can. 31: 327–328.

Carpenter, G. F., E. L. Mansey, and N. H. F. Watson. 1974. Abundance and life history of *Mysis relicta* in the St. Lawrence Great Lakes. J. Fish. Res. Board Can. 31: 319–325.

Carter, J. C. H. 1969. Life cycles of *Limnocalanus macrurus* and *Senecella calanoides*, and seasonal abundance and vertical distributions of various planktonic copepods in Parry Sound, Georgian Bay. J. Fish. Res. Board Can. 26: 2543–2560.

1971. Distribution and abundance of planktonic crustacea in ponds near Georgian Bay (Ontario, Canada) in relation to hydrography and water chemistry. Arch. Hydrobiol. 68: 204–231.

Chandler, D. C. 1940. Limnological studies of Western Lake Erie I. Plankton and certain physico-chemical data of the Bass Islands region from September 1938 to November 1939. Ohio J. Sci. 40: 291–336.

Davis, C. C. 1962. The plankton of the Cleveland harbour area of Lake Erie in 1956–1957. Ecol. Monogr. 32: 209–247.

1966. Plankton studies in the largest great lakes of the world, with special references to the St. Lawrence Great Lakes of North America. Univ. Mich. Great Lakes Res. Div. Publ. 14: 1–36.

1968. The July 1967 zooplankton of Lake Erie. Proc. 11th Conf. Great Lakes Res., Int. Assoc. Great Lakes Res. p. 61–75.

1969. Seasonal distribution, constitution, and abundance of zooplankton in Lake Erie. J. Fish. Res. Board Can. 26: 2459–2476.

Deevey, E. S. Jr., and G. B. Deevey. 1971. The American species of *Eubosmina* Seligo (Crustacea Cladocera). Limnol. Oceanogr. 16: 201–218.

Engel, R. A. 1962. *Eurytemora affinis*, a calanoid copepod new to Lake Erie. Ohio J. Sci. 62: 252.

Faber, D. J., and E. G. Jermolajev. 1966. A new copepod genus in plankton of the Great Lakes. Limnol. Oceanogr. 11: 301–303.

Foulds, J. 1972. Energetics of vertical migration in *Mysis relicta* Lovén 1862 (Crustacea Mysidacea). M.Sc. Thesis. Univ. Guelph, Guelph, Ont. 62 p. (mimeo.)

Frontier, S. 1973. Étude statistique de la dispersion du zooplancton. J. Exp. Mar. Biol. Ecol. 12: 229–262.

Gannon, J. E. 1972. A contribution to the ecology of zooplankton crustacea of Lake Michigan and Green Bay. Univ. Wis. Cent. Great Lakes Stud. p. 1–257 (mimeo.)

Gannon, J. E., and A. M. Beeton. 1971. The decline of the large zooplankter *Limnocalanus macrurus* Sars. (Copepoda Calanoida) in Lake Erie. Proc. 14th Conf. Great Lakes Res., Int. Assoc. Great Lakes Res. p. 27–38.

Gliwicz, Z. M. 1969. The food sources of lake zooplankton. Ekol. Pol. (Ser. B) 15: 205–223.

Hubschman, J. H. 1960. Relative daily abundance of planktonic Crustacea in the Island region of Western Lake Erie. Ohio J. Sci. 60: 335–340.

Jahoda, W. J. 1948. Seasonal differences in the distribution of *Diaptomus* in Western Lake Erie. Ph.D. Thesis. Ohio State Univ., Columbus, Ohio. 100 p. (mimeo.)

Lance, G. W., and W. T. Williams. 1967. A general theory of classificatory sorting strategies I. Hierarchical systems. Comput. Sci. 9: 373–380.

Leach, J. H. 1973. Seasonal distribution, composition and abundance of zooplankton in Ontario waters of Lake St. Clair. Proc. 16th Conf. Great Lakes Res., Int. Assoc. Great Lakes Res. p. 54–64.

McNaught, D. C., and M. Buzzard. 1973. Changes in zooplankton populations in Lake Ontario (1939–1972). Proc. 16th Conf. Great Lakes Res., Int. Assoc. Great Lakes Res. p. 76–96.

MUNAWAR, M., AND A. NAUWERCK. 1971. The composition and horizontal distribution of phytoplankton in Lake Ontario during the year 1970. Proc. 14th Conf. Great Lakes Res., Int. Assoc. Great Lakes Res. p. 69–78.

NAUWERCK, A. 1972. Notes on the rotifers of Lake Ontario. Can. Cent. Inland Waters, Great Lakes Biolimnol. Lab. 37 p. (unpublished)

NAUWERCK, A., G. F. CARPENTER, AND L. DEVEY. 1972. The Crustacean zooplankton of Lake Ontario, 1970. Paper presented at the 15th Conference on Great Lakes Res. 20 p. (mimeo.)

PATALAS, K. 1969. Composition and horizontal distribution of crustacean zooplankton in Lake Ontario. J. Fish. Res. Board Can. 26: 2135–2164.

1972. Crustacean zooplankton and eutrophication of the St. Lawrence Great Lakes. J. Fish. Res. Board Can. 29: 1451–1462.

PORTER, K. G. 1973. Selective grazing and differential digestion of algae by zooplankton. Nature 244: 179–180.

RIGLER, F. H. 1972. Feeding behaviour of *Limnocalanus macrurus*, p. 32–37. *In* Char Lake Project Annual Report, 1972.

ROBERTSON, A. A. 1966. The distribution of calanoid copepods in the Great Lakes. Univ. Mich. Great Lakes Res. Div. Publ. 15: 129–139.

STEPHENSON, W., W. T. WILLIAMS, AND S. D. COOK. 1972. Computer analysis of Petersen's original data on bottom communities. Ecol. Monogr. 42: 387–415.

WATSON, N. H. F., AND G. F. CARPENTER. 1974. Seasonal distribution of crustacean zooplankton and net plankton biomass in lakes Ontario, Erie, and Huron. J. Fish. Res. Board Can. 31: 309–317.

WATSON, N. H. F., G. F. CARPENTER, AND A. NAUWERCK. 1973. Seasonal distribution of Crustacean zooplankton in Lake Erie 1970. Can. Cent. Inland Waters, Great Lakes Biolimol. Lab. 34 p. (unpublished)

WELLS, L. 1960. Seasonal abundance and vertical distribution of planktonic Crustacea in Lake Michigan. U.S. Fish Wildl. Serv. Fish. Bull. 60: 343–369.

1970. Effects of alewife predation on zooplankton populations in Lake Michigan. Limnol. Oceanogr. 15: 556–565.

WILSON, J. B., AND J. C. ROFF. 1973. Seasonal vertical distributions and diurnal migration patterns of Lake Ontario Crustacean zooplankton. Proc. 16th Conf. Great Lakes Res., Int. Assoc. Great Lakes Res. p. 190–203.

Review of Geological Research as it Relates to an Understanding of Great Lakes Limnology[1]

P. G. Sly and R. L. Thomas

Department of the Environment
Environmental Management Service
Canada Centre for Inland Waters Burlington, Ont.

Sly, P. G., and R. L. Thomas. 1974. Review of geological research as it relates to an understanding of Great Lakes limnology. J. Fish Res. Board Can. 31: 795–825.

A review of studies on the geology of recent sediment deposits in the Great Lakes is presented. A summary of quaternary events and a cross-correlation between each of the major basins has been attempted; in this respect it is essential to realize the control imposed upon present depositional conditions by the preceding sedimentary environments (often related to significantly different lake levels). Sediment/energy relations have been discussed, particularly in the context of large lake limnology. Geochemical topics include major and trace metal data, the formation of ferromanganese deposits, and major nutrients (C, N, and P); published material covering these topics is, however, rather limited.

Throughout this review the authors have attempted to show the interrelations between such geological evidence and physical, chemical, and biological processes; further, the application of such information to human oriented problems.

Sly, P. G., and R. L. Thomas. 1974. Review of geological research as it relates to an understanding of Great Lakes limnology. J. Fish. Res. Board Can. 31: 795–825.

Nous passons en revue les travaux effectués sur la géologie des dépôts récents du sédiment des Grands lacs. Nous brossons un tableau des événements du Quaternaire et tentons d'établir une corrélation réciproque entre chacun des bassins majeurs; sous ce rapport, il est essentiel de comprendre le contrôle qu'imposent les environnements sédimentaires antérieurs sur les conditions présentes de déposition, (conditions souvent liées à des niveaux de lac nettement différents). Nous examinons les relations sédiment/énergie, en particulier dans le contexte de la limnologie des lacs de grande étendue. Les topiques géochimiques comprennent des données sur les métaux principaux et les traces de métaux, sur la formation de dépôts de ferromanganèse et sur les substances nutritives majeures (C, N et P); les publications sur ces sujets sont cependant plutôt limitées.

Tout au cours de cette revue, nous tentons de démontrer les relations qui existent entre des données géologiques de cette nature et les processus physiques, chimiques et biologiques; de plus l'application de telles connaissances à des problèmes à orientation humaine.

Accepted January 21, 1974

Geological research, as directed towards Great Lakes studies, has been developed and expanded by at least an order of magnitude during the last decade. In the Great Lakes region this has been nurtured by a number of contributory factors; notably the impact of increased eutrophication in Lake Erie, the impact of sublethal but toxic contaminants in restricted areas, periods of extreme water level fluctuation, and a greatly increased demand for high quality water for multiple uses. More recently problems related to navigational dredging, resource dredging, shoreline stability, and the demand for recreational facilities have further emphasized the need for greatly improved inventory data and better process understandings.

In response, geological studies related to the so-called environmental issues have been greatly increased. Although, in many ways, the Great Lakes System is comparable to the marine environment, the distinct characteristics of an essentially tideless and nonsaline system have led to approaches that are particular to large lake limnology.

Geological studies relating to continuing issues such as bedrock control, regional form, subsurface

---

[1] This paper, part of a special issue that comprises a comprehensive review of Limnology in Canada, was prepared to mark the 19th Congress of the International Association of Limnology (SIL), in Winnipeg, Man., during August 1974.

Printed in Canada (J3288)

structure, and preglacial stratigraphy have of course continued, but without the impetus of immediate concern. This is similarly true of the ongoing research in support of applied fields of the oil and gas industry, the chemical industry (salts), and some water supply (groundwater).

The support of geological studies related to limnology has developed on a broad basis. In the United States, federal agencies such as the Corps of Engineers and (more recently) the Environmental Protection Agency, have contributed widely to work on sediment erosion, transport, and deposition, and general geochemical assessment. Illinois and Ohio have also made major contributions to studies on recent sedimentary environments in both southern Lake Michigan and western Lake Erie. Some of the most significant contributions, however, have come from the universities, and although all Great Lakes states have been involved, Madison (Wis.), Ann Arbor (Mich.), and Rochester (N.Y.), may be considered particularly productive.

In Canada, federal agencies such as the Department of the Environment and Department of Energy Mines and Resources have made major contributions, particularly in the form of lakewide studies. Provincial agencies in Ontario, responsible for mines, natural resources, and environment, have also provided considerable input (frequently in the nearshore areas), and certain independent authorities such as the Toronto Harbour Commissioners have provided a wealth of data in specific areas. Universities, too, have strongly supported geological studies, and the schools at Queen's (Kingston), Toronto, Waterloo, and Western Ontario (London) have had long associations in these fields.

It is perhaps a little ungenerous to single out individual research establishments, but on the other hand, a general indication of the sources of research information may help the reader to better appreciate its availability, and to indicate where such may be most profitably sought.

The following review has been compiled on the basis of a number of related topics which most clearly indicate the development of recent geological studies. Although primarily selective, every attempt has been made to give as representative a view as can be obtained from the existing literature and personal communications. The authors regret the many omissions necessary, which reflect the difficulties inherent in separating out the geologically oriented components from the essentially integrated limnologic studies of the Great Lakes, and condensing such material.

The following specific topics have been chosen for attention: the quaternary history, the distributions of surficial sediments in relation to energy controlled processes, the major element geochemistry and the influence of textural parameters, trace metal geochemistry (with particular emphasis on the presence of mercury), the occurrence of ferromanganese nodules and concretions, the significance of carbon, phosphorus, and nitrogen distributions, and an assessment as to where the future trends of research may lead.

Quaternary History of the Great Lakes Region

The form and occurrence of the Great Lakes is strongly controlled by the underlying bedrock geology, the most significant elements of which are illustrated in Fig. 1 and 2. For more detailed information, however, reference should be made to Hough (1958), and Douglas (1970).

Although undoubted elements of preglacial drainage systems have been recorded from the Great Lakes region, modification of this presumed Tertiary drainage pattern by ice-scour, fill, reworking, and interglacial rechannelling has left the pattern unclear and open to multiple interpretation. Despite such highly conjectural information, however, it may be suggested that Proto-Lake Huron and Georgian Bay drained into Proto-Lake Ontario, near Toronto, and that Proto-Lake Erie may also have drained into Proto-Lake Ontario, near the present western end of the lake (Hamilton). Almost certainly the whole system drained out through a Proto-St. Lawrence valley, much as at present (Sly and Lewis 1972).

In North America four glacial stages and three interglacials are recognized:

Stage	*Interglacial*
Wisconsin	(Recent nonglacial interval)
Illinois	Sangamon
Kansan	Yarmouth
Nebraskan	Aftonian

Of these, only three stages have been clearly identified (in the lower lakes area), namely: Illinoian, Sangamon, and Wisconsin, and substantive data have been drawn from the Toronto (and Woodbridge, lying a little to the north) and Niagara areas of Lake Ontario, and from Port Stanley on the north shore of Lake Erie. Although deposits of pre-Illinoian age were almost certainly formed in most of the Great Lakes basin, almost all evidence of them has been obliterated by the effects of subsequent glacial and interglacial events.

Figures 4 and 5 show the quaternary correlation which has been constructed for the Great Lakes basin area, including the upper and lower lakes, and the St. Lawrence Valley. This correlation has been largely derived from the works of Hough (1955), Karrow et al. (1961, 1969), Broecker and Farrand (1963), Dreimanis (1969), Farrand (1969), Hobson and Terasmae (1969), Lewis (1969), Gadd (1971), Dell (1972), and Dreimanis et al. (1972).

In reviewing this data, two major issues become immediately clear: 1) the lack of comparable data much before 15,000 years BP (Before Present) throughout all the upper lakes, and 2) the extreme complexity of events in the Great Lakes Basin during the Wisconsin and subsequently, which reflect massive changes in lake levels over very short (geological) time spans — related to the various controls exerted by both ice fronts and isostatic rebound.

Ontario Basin — During the latter part of the late Wisconsin Stage a complex of peripheral tills was laid down in the Ontario Basin in response to ice movements both from the north and from within the Basin area (itself acting as a local ice center). As the ice melted, high level (Iroquois) glaciolacustrine lakes formed which generally drained south into the Mohawk–Hudson Valley System. At some time just before 11,000 years BP, ice-plugging in the St. Lawrence Valley cleared and lake levels in the Ontario Basin dropped rapidly to a temporary low phase (Admiralty), Lewis

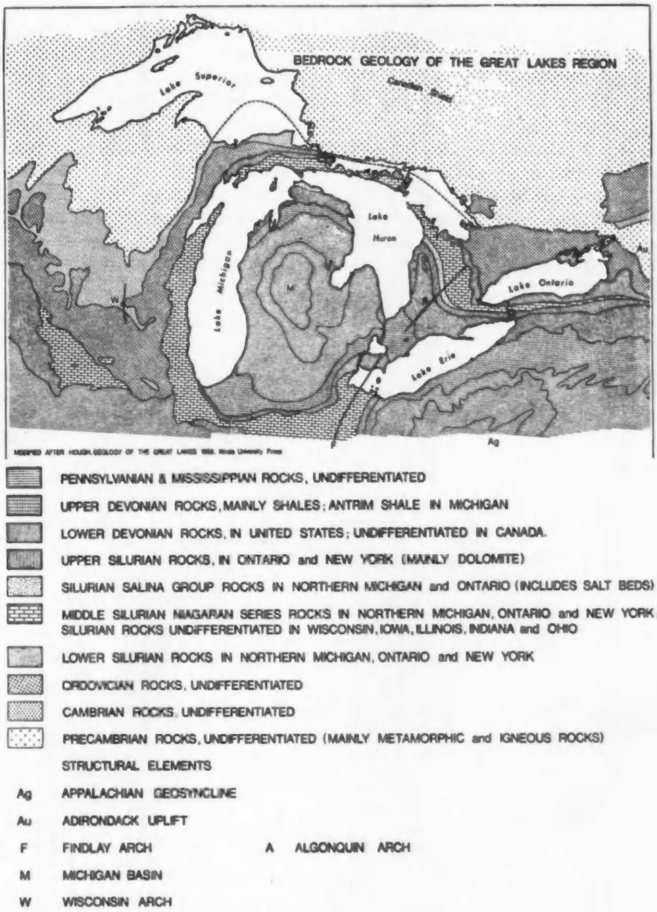

BEDROCK GEOLOGY OF THE GREAT LAKES REGION
Lake Superior
Canadian Shield
Lake Michigan
Lake Huron
Lake Ontario
Lake Erie
M
W
Au
Ag
F
MODIFIED AFTER HOUGH, GEOLOGY OF THE GREAT LAKES 1958, Illinois University Press
PENNSYLVANIAN & MISSISSIPPIAN ROCKS, UNDIFFERENTIATED
UPPER DEVONIAN ROCKS, MAINLY SHALES; ANTRIM SHALE IN MICHIGAN
LOWER DEVONIAN ROCKS, IN UNITED STATES; UNDIFFERENTIATED IN CANADA.
UPPER SILURIAN ROCKS, IN ONTARIO and NEW YORK (MAINLY DOLOMITE)
SILURIAN SALINA GROUP ROCKS IN NORTHERN MICHIGAN and ONTARIO (INCLUDES SALT BEDS)
MIDDLE SILURIAN NIAGARAN SERIES ROCKS IN NORTHERN MICHIGAN, ONTARIO and NEW YORK; SILURIAN ROCKS UNDIFFERENTIATED IN WISCONSIN, IOWA, ILLINOIS, INDIANA and OHIO
LOWER SILURIAN ROCKS IN NORTHERN MICHIGAN, ONTARIO and NEW YORK
ORDOVICIAN ROCKS, UNDIFFERENTIATED
CAMBRIAN ROCKS, UNDIFFERENTIATED
PRECAMBRIAN ROCKS, UNDIFFERENTIATED (MAINLY METAMORPHIC and IGNEOUS ROCKS)
STRUCTURAL ELEMENTS
Ag APPALACHIAN GEOSYNCLINE
Au ADIRONDACK UPLIFT
F FINDLAY ARCH
A ALGONQUIN ARCH
M MICHIGAN BASIN
W WISCONSIN ARCH

FIG. 1. Bedrock geology of the Great Lakes region.

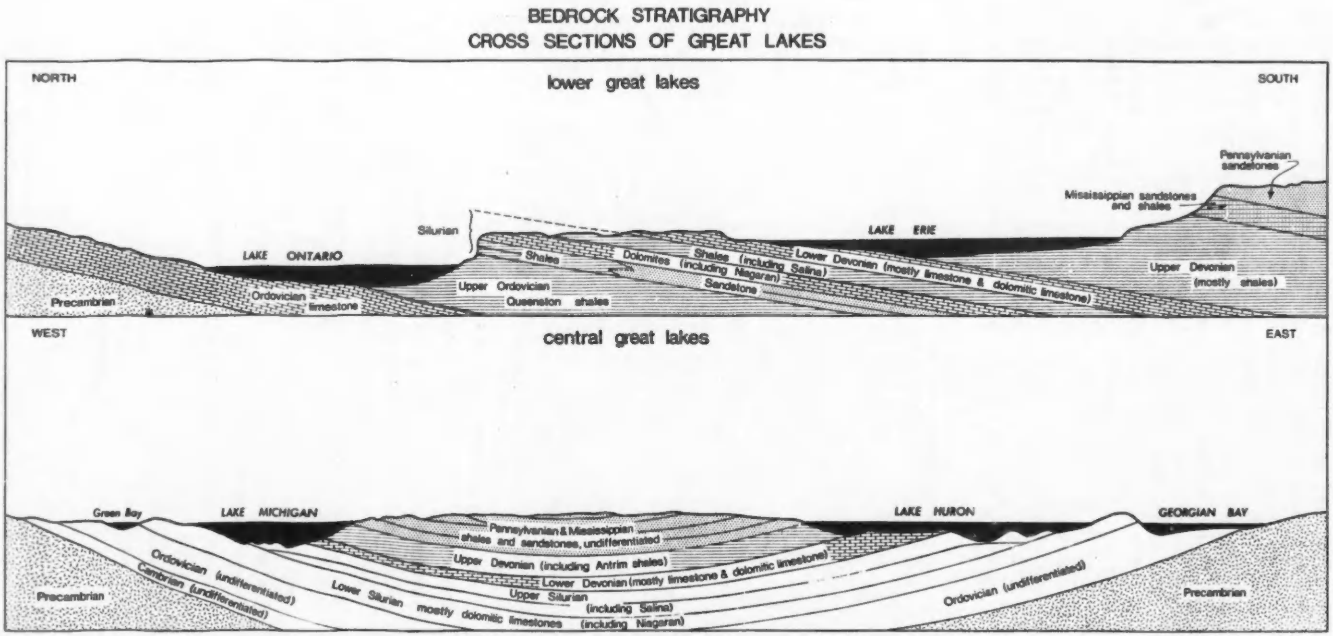

BEDROCK STRATIGRAPHY
CROSS SECTIONS OF GREAT LAKES
NORTH
lower great lakes
SOUTH
Pennsylvanian sandstones
Mississippian sandstones and shales
LAKE ERIE
Silurian
LAKE ONTARIO
Shales
Dolomites (including Niagaran)
Shales (including Salina)
Lower Devonian (mostly limestone & dolomitic limestone)
Upper Devonian (mostly shales)
Sandstone
Upper Ordovician
Queenston shales
Precambrian
Ordovician limestone
WEST
central great lakes
EAST
Green Bay
LAKE MICHIGAN
LAKE HURON
GEORGIAN BAY
Pennsylvanian & Mississippian shales and sandstones, undifferentiated
Upper Devonian (including Antrim shales)
Lower Devonian (mostly limestone & dolomitic limestone)
Upper Silurian (including Salina)
Lower Silurian mostly dolomitic limestones (including Niagaran)
Ordovician (undifferentiated)
Cambrian (undifferentiated)
Precambrian
Ordovician (undifferentiated)
Precambrian

FIG. 2. Bedrock stratigraphy cross sections of Great Lakes.

(1969a) which drained eastwards through the St. Lawrence Valley. Contemporary sea levels were relatively high and it is possible that salt water conditions then persisted almost immediately east of Kingston (in the St. Lawrence Valley). Subsequently, and certainly during the last 10,000–11,000 years, isostatic rebound has caused the control sill of Lake Ontario (near Kingston) to rise, at a rate presently estimated at 0.37 m per century. This has effectively deepened the lake and raised the water level (relative to the west end of the lake) by something in excess of 80 m, due largely to differential isostatic rebound.

Erie Basin — Deglaciation in the Erie Basin (probably because of its more southerly latitude and also because of the general shallowness of the depression) began earlier and, despite minor glacial advances associated with both the Cary and Port Huron stadials, high level glaciolacustrine lakes were already forming more than 1000 yr before those in the Ontario Basin.

The early Maumee Lake phases (the level of Maumee III is recorded at 238 m APSL — above present sea level) drained southwest into the Mississippi System through the Maumee River Valley (western Lake Erie), subsequently Lake Arkona (216–212 m APSL), Lake Whittlesey (225 m APSL), Lake Warren (204 m APSL), and lakes Grassmere and Lundy (195–189 m APSL), all drained westwards into the Mississippi System via Lake Michigan (mostly through the Saginaw Bay depression in the Huron Basin). Early Lake Erie, however, dropped rapidly to a low level (142 m APSL) with the opening of the Niagara Gorge and subsequently drained eastwards into Lake Iroquois in the Ontario Basin. As in the Ontario Basin, differential isostatic uplift has caused the eastern end of the Basin to rise relative to the western end, and lake levels have risen approximately 33 m during the past 12,000 yr.

Huron and Georgian Bay Basin — It appears, during the late Wisconsin Cary Stadial and subsequent Cary–Port Huron Interstadial periods, that ice-fronted lakes formed in the extreme southern part of Lake Huron and adjacent (depressed) area of Saginaw Bay. Ice retreat continued and the basin was generally ice free by about 12,000 years BP, although a subsequent minor ice advance related to the Valders Stadial (?), or surge, affected the extreme north and northwestern (Straits of Mackinac) areas of the basin.

While the ice front stood to the north of the main part of the Huron and Michigan basins, waters were ponded at high levels (in excess of 183 m APSL)

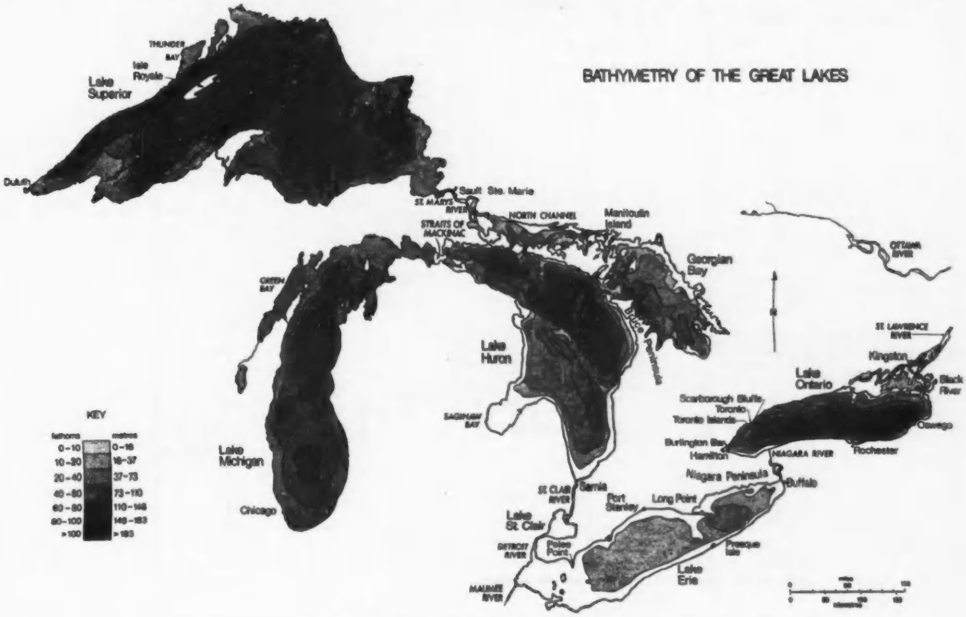
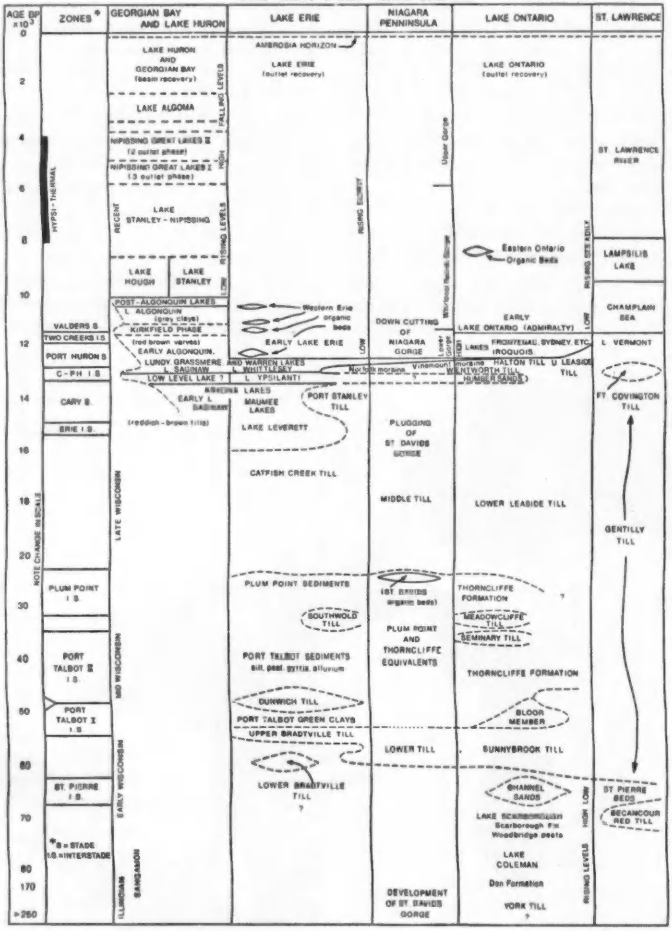

BATHYMETRY OF THE GREAT LAKES
THUNDER BAY
Isle Royale
Lake Superior
Duluth
Sault Ste. Marie
ST. MARYS RIVER
STRAITS OF MACKINAC
NORTH CHANNEL
Manitoulin Island
Georgian Bay
Bruce Peninsula
OTTAWA RIVER
ST. LAWRENCE RIVER
Kingston
Lake Ontario
Black River
Oswego
Rochester
Scarborough Bluffs
Toronto
Toronto Islands
Burlington Bay
Hamilton
NIAGARA RIVER
Niagara Peninsula
Buffalo
GREEN BAY
Lake Huron
SAGINAW BAY
Lake Michigan
Chicago
ST. CLAIR RIVER
Sarnia
Port Stanley
Long Point
Lake St. Clair
DETROIT RIVER
Pelee Point
Presque Isle
Lake Erie
MAUMEE RIVER
KEY
fathoms
metres
0–10 0–18
10–20 18–37
20–40 37–73
40–60 73–110
60–80 110–146
80–100 146–183
>100 >183
miles
0 50 100
0 50 100 150
kilometres

FIG. 3. Bathymetry of the Great Lakes

and effectively coalesced into one vast system, Lake Algonquin, which drained both south and east; through an outlet near Chicago, through the St. Clair–Detroit–Lake Erie and Niagara System to Lake Iroquois in the Ontario Basin, and through the southern part of Georgian Bay which also drained into Lake Iroquois. Lake Chicago in the Michigan Basin was temporarily cut off from the main Algonquin Lake during the Valders ice advance. Following this, the ice continued to retreat and after the rejoining of Michigan and Huron basins, water levels dropped rapidly as a new northerly outlet (now clear of ice) allowed drainage eastwards through the Ottawa River Valley (from Georgian Bay). Also at this time flow between Huron and Erie basins may have ceased.

Water levels in the upper lakes continued to drop to the contemporaneous low stages of lakes Stanley, Hough, and Chippewa. Slowly, however, the effects of isostatic rebound began to affect the

QUATERNARY CORRELATION IN THE GREAT LAKES REGION CANADA – LOWER LAKES


AGE BP ×10³
ZONES*
GEORGIAN BAY AND LAKE HURON
LAKE ERIE
NIAGARA PENNINSULA
LAKE ONTARIO
ST. LAWRENCE
0
2
4
6
8
10
12
14
16
18
20
30
40
50
60
70
80
170
>250
NOTE CHANGE IN SCALE
HYPSI-THERMAL
VALDERS S
TWO CREEKS I.S.
PORT HURON S
C-PH I.S.
CARY S.
ERIE I.S.
PLUM POINT I.S.
PORT TALBOT II I.S.
PORT TALBOT I I.S.
ST. PIERRE I.S.
*S = STADE
I.S. = INTERSTADE
RECENT
LATE WISCONSIN
MID WISCONSIN
EARLY WISCONSIN
ILLINOIAN
SANGAMON
LAKE HURON AND GEORGIAN BAY (basin recovery)
LAKE ALGOMA
NIPISSING GREAT LAKES II (2 outlet phase)
NIPISSING GREAT LAKES I (3 outlet phase)
LAKE STANLEY - NIPISSING
LAKE HOUGH
LAKE STANLEY
FALLING LEVELS
HIGH
RISING LEVELS
LOW
POST-ALGONQUIN LAKES
L. ALGONQUIN (grey clays)
KIRKFIELD PHASE
(red brown varves)
EARLY ALGONQUIN.
LUNDY GRASSMERE AND WARREN LAKES
L. SAGINAW
L. WHITTLESEY
LOW LEVEL LAKE ?
L. YPSILANTI
ARKONA LAKES
EARLY L. SAGINAW
MAUMEE LAKES
(reddish-brown till)
AMBROSIA HORIZON
LAKE ERIE (outlet recovery)
RISING SLOWLY
Western Erie organic beds
EARLY LAKE ERIE
LOW
PORT STANLEY TILL
LAKE LEVERETT
CATFISH CREEK TILL
PLUM POINT SEDIMENTS
SOUTHWOLD TILL
PORT TALBOT SEDIMENTS silt, peat, gyttja, alluvium
DUNWICH TILL
PORT TALBOT GREEN CLAYS
UPPER BRADTVILLE TILL
LOWER BRADTVILLE TILL
?
Upper Gorge
Whirlpool Rapids Gorge
Lower Gorge
DOWN CUTTING OF NIAGARA GORGE
Norfolk moraine
Vinemount moraine
?
PLUGGING OF ST DAVIDS GORGE
MIDDLE TILL
(ST DAVIDS organic beds)
PLUM POINT AND THORNCLIFFE EQUIVALENTS
LOWER TILL
DEVELOPMENT OF ST DAVIDS GORGE
LAKE ONTARIO (outlet recovery)
Eastern Ontario Organic Beds
RISING STEADILY
EARLY LAKE ONTARIO (ADMIRALTY)
LOW
HIGH
LAKES FRONTENAC, SYDNEY, ETC. IROQUOIS
HALTON TILL
U LEASIDE TILL
WENTWORTH TILL
HUMBER SANDS
LOWER LEASIDE TILL
THORNCLIFFE FORMATION
?
MEADOWCLIFFE TILL
SEMINARY TILL
THORNCLIFFE FORMATION
BLOOR MEMBER
SUNNYBROOK TILL
CHANNEL SANDS
LAKE SCARBOROUGH
Scarborough Fm
Woodbridge peats
LAKE COLEMAN
Don Formation
YORK TILL
?
HIGH LOW
RISING LEVELS
ST. LAWRENCE RIVER
LAMPSILIS LAKE
CHAMPLAIN SEA
L. VERMONT
FT. COVINGTON TILL
GENTILLY TILL
ST PIERRE BEDS
BECANCOUR RED TILL

AFTER SLY AND LEWIS I.G.C. GUIDEBOOK A 42 1972 MONTREAL

FIG. 4. Quaternary correlation in the Great Lakes region Canada lower lakes.

area, and as the eastern outlet sills began to rise, the newly rising levels of the Nipissing System began to take effect.

At its maximum development, the Nipissing III System incorporated all the Superior, Michigan, Huron, and Georgian Bay waters as a single vast lake (with the Sault Ste. Marie sill at the south end of Lake Superior completely submerged); drainage was simultaneously effected through the Chicago, St. Clair–Detroit, and Ottawa River outlets.

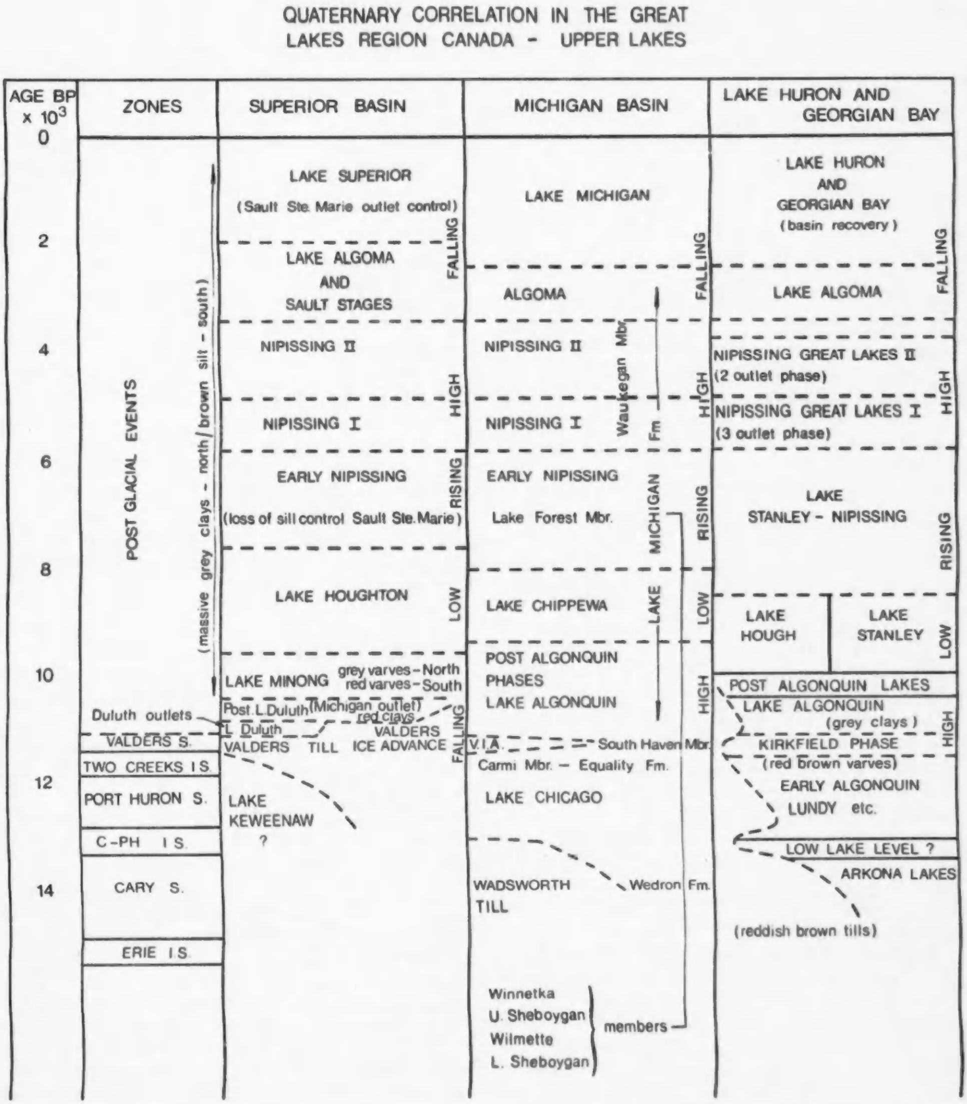

QUATERNARY CORRELATION IN THE GREAT LAKES REGION CANADA - UPPER LAKES
AGE BP x 10³
0
2
4
6
8
10
12
14
ZONES
SUPERIOR BASIN
MICHIGAN BASIN
LAKE HURON AND GEORGIAN BAY
POST GLACIAL EVENTS
(massive grey clays - north / brown silt - south)
Duluth outlets
VALDERS S.
TWO CREEKS I.S.
PORT HURON S.
C-PH I.S.
CARY S.
ERIE I.S.
LAKE SUPERIOR
(Sault Ste. Marie outlet control)
LAKE ALGOMA AND SAULT STAGES
FALLING
NIPISSING II
HIGH
NIPISSING I
EARLY NIPISSING
(loss of sill control Sault Ste. Marie)
RISING
LAKE HOUGHTON
LOW
LAKE MINONG
grey varves - North
red varves - South
Post. L. Duluth
(Michigan outlet)
red clays
L. Duluth
VALDERS TILL
VALDERS ICE ADVANCE
FALLING
LAKE KEWEENAW ?
LAKE MICHIGAN
ALGOMA
FALLING
NIPISSING II
Waukegan Mbr.
NIPISSING I
HIGH
Fm.
EARLY NIPISSING
Lake Forest Mbr.
MICHIGAN
RISING
LAKE CHIPPEWA
LAKE
LOW
POST ALGONQUIN PHASES
LAKE ALGONQUIN
HIGH
V.I.A.
South Haven Mbr.
Carmi Mbr. - Equality Fm.
LAKE CHICAGO
WADSWORTH TILL
Wedron Fm.
Winnetka
U. Sheboygan
Wilmette
L. Sheboygan
members
LAKE HURON AND GEORGIAN BAY
(basin recovery)
FALLING
LAKE ALGOMA
NIPISSING GREAT LAKES II
(2 outlet phase)
HIGH
NIPISSING GREAT LAKES I
(3 outlet phase)
LAKE STANLEY - NIPISSING
RISING
LAKE HOUGH
LAKE STANLEY
LOW
POST ALGONQUIN LAKES
LAKE ALGONQUIN
(grey clays)
HIGH
KIRKFIELD PHASE
(red brown varves)
EARLY ALGONQUIN
LUNDY etc.
LOW LAKE LEVEL ?
ARKONA LAKES
(reddish brown tills)

FIG. 5. Quaternary correlation in the Great Lakes region Canada upper lakes.

However, with continued differential isostatic rebound, the Ottawa River outlet closed and lake levels dropped slightly.

Following a further slight adjustment of water levels, due to closure of the Chicago outlet, the Algoma Phase came into existence.

More recent changes in the Upper Lakes levels have been influenced by minor changes in the erosion level of the outlet sill of the St. Clair River.

Michigan Basin — The southern part of the Michigan Basin began to develop ice-fronted glaciolacustrine conditions abou tthe same time as the Erie Basin, but early stages of high level Lake Chicago (195 m APSL) were not as extensive as those of the Erie Basin; they drained south into the Mississippi System, through the Chicago outlet. An early connection between Huron and Michigan basins formed through the Saginaw Bay depression, but the Straits of Mackinac connection was not opened until the onset of the Algonquin Phase. The subsequent Valders ice advance effectively reglaciated the northern half of the lake (temporarily reforming the ice-ponded Lake Chicago), but this did not last long. Although the Saginaw Bay area was ice-free, it does not appear that linkage across this depression was reestablished at this time. The post-Valders development of the Michigan Basin may be considered synonymous with that of the Huron Basin.

Superior Basin — The first area of the Superior Basin to become ice-free was around Duluth, at its western end. A high-level, ponded lake (Keweenaw) is believed to have formed at about 331 m APSL, with its beginnings perhaps as early as the Cary–Port Huron Interstadial. The subsequent Valders ice advance completely refilled the basin and only after the retreat of this ice mass does a history of events remain clearly defined. Lake Duluth formed largely in the image of the previously conceived Lake Keweenaw, and drained westwards through high level outlets near Duluth.

As ice retreat continued, lower outlets were first established in the north end of Green Bay (Michigan Basin) and later through Sault Ste. Marie, which provided drainage for the falling levels of Lake Minong.

The Superior Basin, like those of the other upper Great Lakes also had an extreme low-level phase, Lake Houghton, which was approximately contemporaneous with Lake Chippewa. The Nipissing and Algoma phases were also shared with the upper Great Lakes, and not until about 2000 yr ago did the reestablishment of the outlet-sill control at Sault Ste. Marie bring into existence the form of Lake Superior that we know today.

Postglacial Lake Deposits

From the preceding outline, a series of events may be established, more or less typical of postglacial conditions throughout the Great Lakes region: 1) Deposition of last glacial tills; 2) Formation of high level lakes, usually ponded by retreating ice front; 3) Collapse of remaining ice barriers and fall of lake levels to very low elevation; 4) Differential isostatic rebound, selective recovery of outlets, rising lake levels; 5) Post-Nippissing adjustments (including falling levels) in the upper lakes.

In terms of sedimentary sequences the following general correlations can be made, against the above enumeration (excluding 1):

2) Deposition of glaciolacustrine sequences, often varved clays, with occasional ice-rafted erratics; mostly clay materials derived from reworking of exposed glacial tills. The formation of occasional ice-front moraines during periods of frontal stand, and the development of coarse sand and gravel beach and shoal deposits, which now lie mostly well outside the existing lake boundary (having formed in relation to extreme high-level episodes).

3) Continued deposition of fine clayey sediments (rarely varved), in the more central and deepest parts of the lake basins; with the formation of peripheral shallow-water deposits, now found at variously submerged depths considerably below present lake level. First developments of organic deposits (peats and bog materials) coincident with extreme low lake levels and ameliorating climatic conditions.

4) Continued deposition of midlake fine clays, and formation of transgressive mud and silty sand deposits. The development of transgressive peripheral high energy (sand and gravel) deposits, and their continued development sustained by reworking and subjection of new sources; occasionally such deposits now occur as subaqueous lag materials, their continued existence being cut short by reduction of unconsolidated source material exposed to the influence of wave attack. The inundation of forest zones and of more organic rich layers by rising water levels.

5) Formation of recent high-level beaches (below the "Algonquin" levels), and adjustment to present sedimentary conditions.

SELECTED REGIONAL EXAMPLES

Rather than detailing the stratigraphic sequence in each lake basin, a series of examples has been selected to illustrate some of the better preserved sequences. Although a number of authors (Dreimanis and Terasmae 1958; Karrow 1967; Prest 1970;

Lewis and Sly 1971) have discussed the late Wisconsin sequences at Toronto, Niagara (Hobson and Terasmae 1969), and Port Stanley (Dreimanis 1969) such detail may not be so generally typical.

In Lake Michigan, Gross et al. (1972) detailed the presence of the Wadsworth till in the surrounding basin, and its occurrence as the Wedron Formation within the basin. This material is typically a compact blue-grey clay and clayey silty till with low water content (25%) and traces of sand and pebbles, of irregular thickness, and which overlies the bedrock directly.

Overlying this till, which is considered to be an ice contact deposit, is the Carmi Member, a glaciolacustrine deposit correlated with the two Creeks Interstadial. The Carmi Member is compositionally *identical to the Wedron Formation (typically* rich in Illite), is relatively thin, and tends to flatten out irregularities in the underlying till. Both sandy and clayey end-member facies are present and are correlated with the development of ice-fronted Lake Chicago. Both Wedron and Carmi materials are considered to be largely "locally" derived.

During the Valders Stadial (?), glacial cover readvanced, bringing with it the typically red clayey till materials derived from the Canadian Shield region, which effectively formed the latest glacial deposit in much of the Michigan Basin, all of Superior, and the most northerly parts of the Huron and Georgian Bay basins.

While the Valders till was deposited in the northern part of the Michigan Basin reddish-grey, very fine grained clays (up to 98% less than 2 μm) were deposited subaqueously to the south (water content up to 124%). These clays (South Haven Member) also contained some gravel and were obviously deposited (largely under surface ice cover) contemporaneously with the Valders material. Despite the fact that the Valders till has a significant carbonate composition, this is noticeably absent in the South Haven deposits. It has been argued that this may have been caused by the dissolving of carbonate fractions in very cold water in combination with very slow sedimentation rates of the fine particulates.

Immediate postglacial deposits (contemporaneous with Duluth and Algonquin phases) show considerable compositional similarity with the Valders till; the more massive reddish clays of the Sheboygan Members are also typified by iron chlorites. The carbonate content too, tends to increase, perhaps reflecting increasing water temperature.

The presence of submerged peat and forest deposits at depth confirms the development of the Lake Chippewa Phase; and subsequent organic rich clays and silts of the Lake Forest Member suggest increasing bioproductivity in the basin, *strongly indicative of climatic amelioration during* the Hypsithermal period. The increase in magnesium in the chlorite fraction is also indicative that the later deposits drew less on the Valders material as a source.

Dell (1972) described the postglacial deposition of sediments in the Superior Basin, and an analogy with the Michigan Basin is clear; the synopsis is summarized as follows: during the early stages of deglaciation when only the southern half of the lake was open, a brown sand associated with the tills was deposited together with massive red clays; overlying these were deposited red varved clays. As the ice retreated further, grey varved clays began to be deposited over extensive parts of the lake, reflecting derivation from the central north shore of Lake Superior. It appears that these varves were related to cyclic (annual) dissolving of the carbonate fraction, and therefore bear many similarities to the carbonate-poor clays of the Michigan Basin.

After the ice had retreated from the northern shore, sediment supply was greatly diminished, varve formation ceased, and massive grey and noncalcerous clays were deposited over most of the northern half of the lake; over the southern part of the lake, brown silty sediments floor most of the lake with a few peripheral sand deposits nearshore.

With reference to Fig. 4 and 5, it may be seen that the early Michigan and Superior sequences are fairly typical of large parts of the Great Lakes Basin.

The widespread occurrence of various organic horizons, additionally, in Georgian Bay (authors' unpublished data), Lake Erie (Lewis 1969), and Ontario (Lewis and McNeely 1967), adds further support to this contention.

The existence of low lake stage deposits of different facies may also be illustrated by examples from the Huron–Georgian Bay area, and Lake Ontario. Figure 6 shows in outline the form of low level lakes Stanley and Hough. This should be compared to Fig. 7 which shows the general sediment distribution in the Great Lakes. More specifically, reference should be made to the original publication (Thomas et al. 1973) on Lake Huron, for comparison of the distribution of the deepest basin muds — type B and type A, with the Stanley–Hough outline; the correlation is remarkable, particularly as the low level lake outlines were computed independently from contour isobase data, and the sediment distribution from sample controlled echograms.

Figure 8 illustrates the sediment sequence as observed in the Kingston region of Lake Ontario, and the presence of reworked, submerged, sandy beach deposits of the low level Admiralty Phase is clearly evident; these deposits were located by echosounding, sampling, and underwater photography. Similar deep sandy (or coarser) deposits have been recorded at greater depth in western Lake Ontario (Lewis 1969a) and further discussed by Lewis and Sly (1971). These deposits are coincident with the Admiralty Phase, also plotted independently from isobase data. Woodrow et al. (1967) reported a drowned beach near Rochester which could also relate to a similar water plane.

Figure 7 illustrates the distribution of the major sediment lithological types in the Great Lakes region, and the separation of each of the major lake basins into a number of smaller sub-basins is clearly evident.

For example, Lake Ontario may be divided into four separate units, and Lake Erie into three major units. These separations reflect the presence of underlying bedrock or glacial controls and further illustrate the significance of even slight bathymetric relief on the present sedimentary environment. This is particularly true in the case of Lake Erie, where the dominance of morainic features is exemplified by comparison of Fig. 7 and 9.

In the lower Great Lakes (Ontario and Erie) water levels have continued to rise for some 11,000 yr; in the upper lakes, however, Nipissing and Algoma phases (since about 6000 years BP) occurred at levels considerably above present water level. The profile schematic of Fig. 10 illustrates the development of the comparable, recent high level beaches and erosion surfaces so developed.

At the present time water levels in the Great Lakes are relatively static, though isostatic rebound continues. However, at some distant point in time, future down-cutting of the Niagara Gorge and northward advance of the Mississippi watershed may significantly alter the form of the lakes.

Today, shoreline erosion and sand transport in the nearshore zone is a significant process in all parts of the Great Lakes (particularly in areas of unconsolidated shoreline material). Offshore slit deposits are accumulating, particularly near urban or heavy agricultural runoff sources. In midlake areas, soft structureless muds are most iyptcal, the carbon content of which is strongly related to the bioproductivity of the overlying waters. The organic carbon content of Superior and Huron

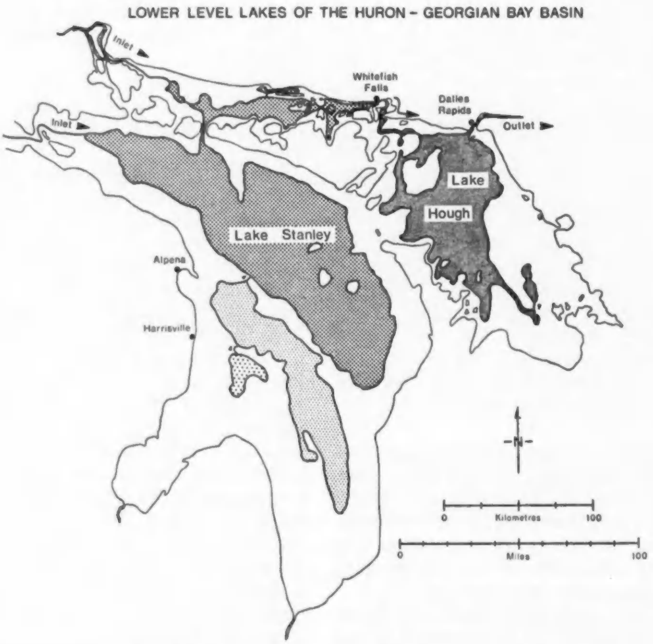


FIG. 6. Lower level lakes of the Huron–Georgian Bay Basin. (After Sly and Lewis, I. G. C. Guidebook A 42, Montreal, (1972).

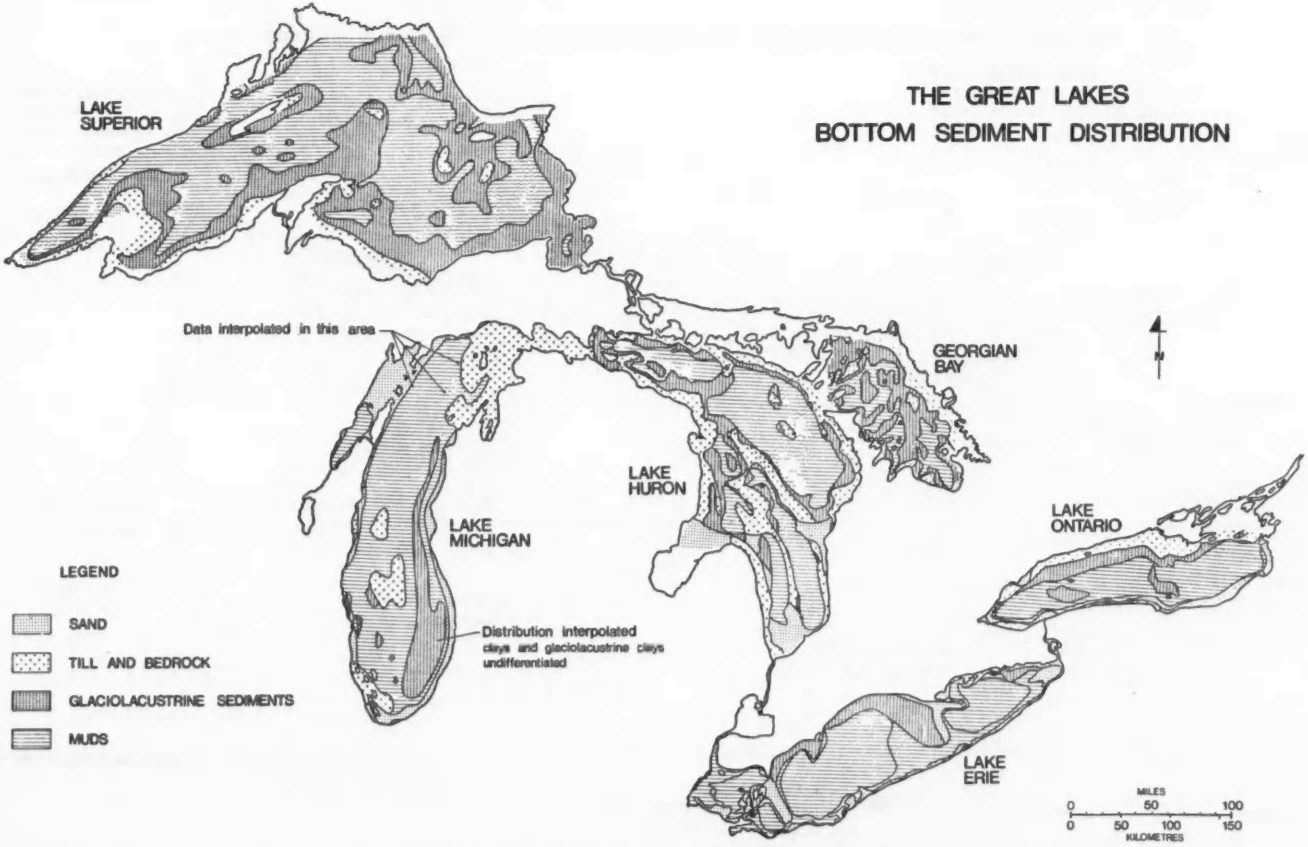

THE GREAT LAKES
BOTTOM SEDIMENT DISTRIBUTION
LAKE SUPERIOR
LAKE MICHIGAN
LAKE HURON
GEORGIAN BAY
LAKE ONTARIO
LAKE ERIE
N
Data interpolated in this area
Distribution interpolated clays and glaciolacustrine clays undifferentiated
LEGEND
SAND
TILL AND BEDROCK
GLACIOLACUSTRINE SEDIMENTS
MUDS
MILES
0 50 100
0 50 100 150
KILOMETRES

FIG. 7. The Great Lakes bottom sediment distribution.

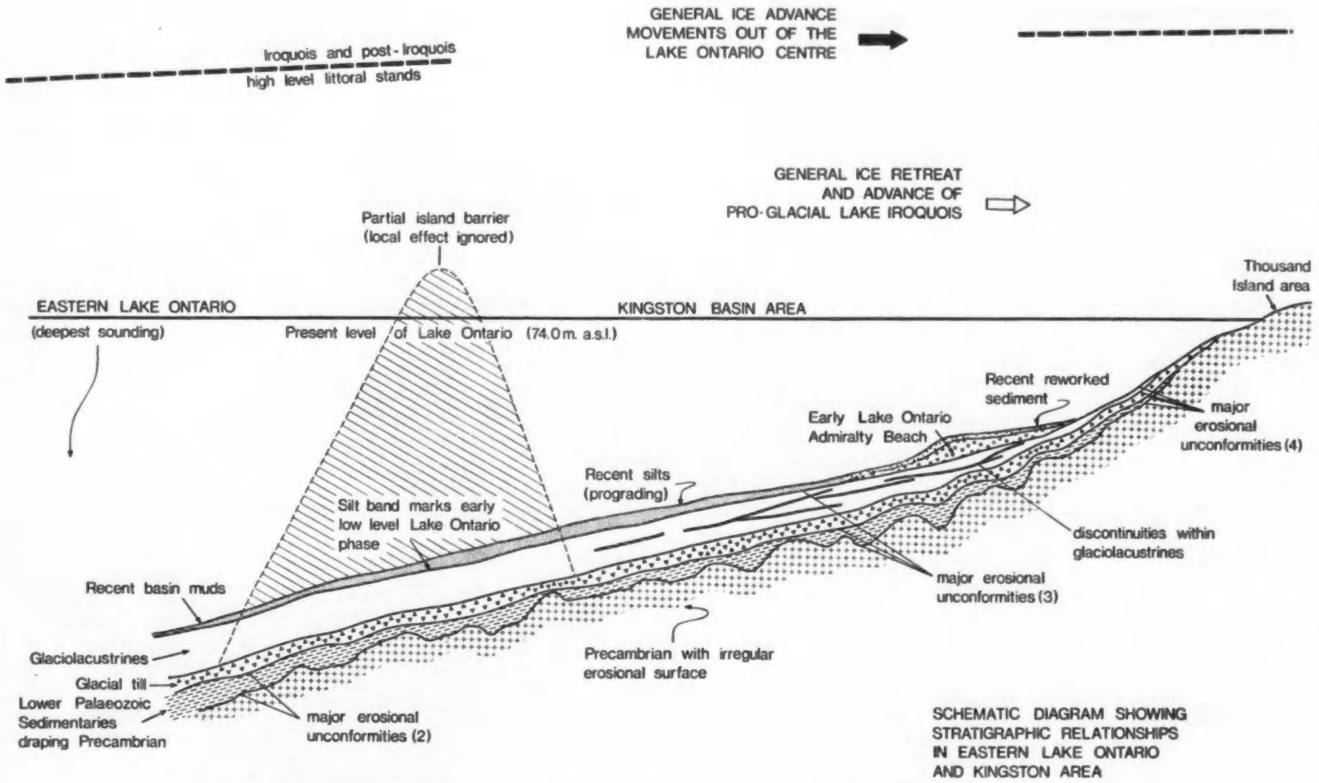

Iroquois and post-Iroquois
high level littoral stands
GENERAL ICE ADVANCE MOVEMENTS OUT OF THE LAKE ONTARIO CENTRE
GENERAL ICE RETREAT AND ADVANCE OF PRO-GLACIAL LAKE IROQUOIS
Partial island barrier (local effect ignored)
Thousand Island area
EASTERN LAKE ONTARIO
KINGSTON BASIN AREA
(deepest sounding)
Present level of Lake Ontario (74.0 m a.s.l.)
Recent reworked sediment
Early Lake Ontario Admiralty Beach
major erosional unconformities (4)
Recent silts (prograding)
Silt band marks early low level Lake Ontario phase
discontinuities within glaciolacustrines
major erosional unconformities (3)
Recent basin muds
Glaciolacustrines
Glacial till
Lower Palaeozoic Sedimentaries draping Precambrian
Precambrian with irregular erosional surface
major erosional unconformities (2)
SCHEMATIC DIAGRAM SHOWING STRATIGRAPHIC RELATIONSHIPS IN EASTERN LAKE ONTARIO AND KINGSTON AREA

FIG. 8. **Schematic diagram showing stratigraphic relationships in eastern Lake Ontario and Kingston area.**

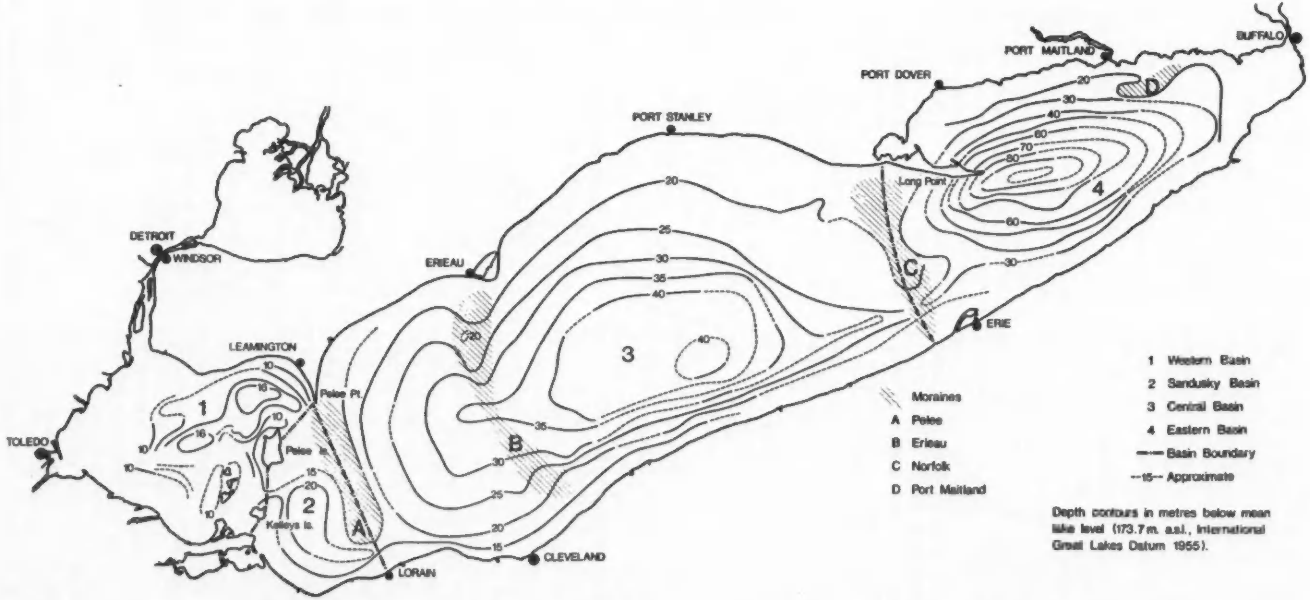

BUFFALO
PORT MAITLAND
PORT DOVER
PORT STANLEY
DETROIT
WINDSOR
ERIEAU
LEAMINGTON
TOLEDO
Pelee Pt.
Pelee Is.
Kelleys Is.
LORAIN
CLEVELAND
ERIE
Long Point
1
2
3
4
A
B
C
D
10
15
20
25
30
35
40
60
70
80
Moraines
A Pelee
B Erieau
C Norfolk
D Port Maitland
1 Western Basin
2 Sandusky Basin
3 Central Basin
4 Eastern Basin
Basin Boundary
--15-- Approximate
Depth contours in metres below mean lake level (173.7 m. a.s.l., International Great Lakes Datum 1955).

FIG. 9. Inferred bathymetry of early Lake Erie showing moraines. Contours drawn on top of glacial deposits relative to present lake level.

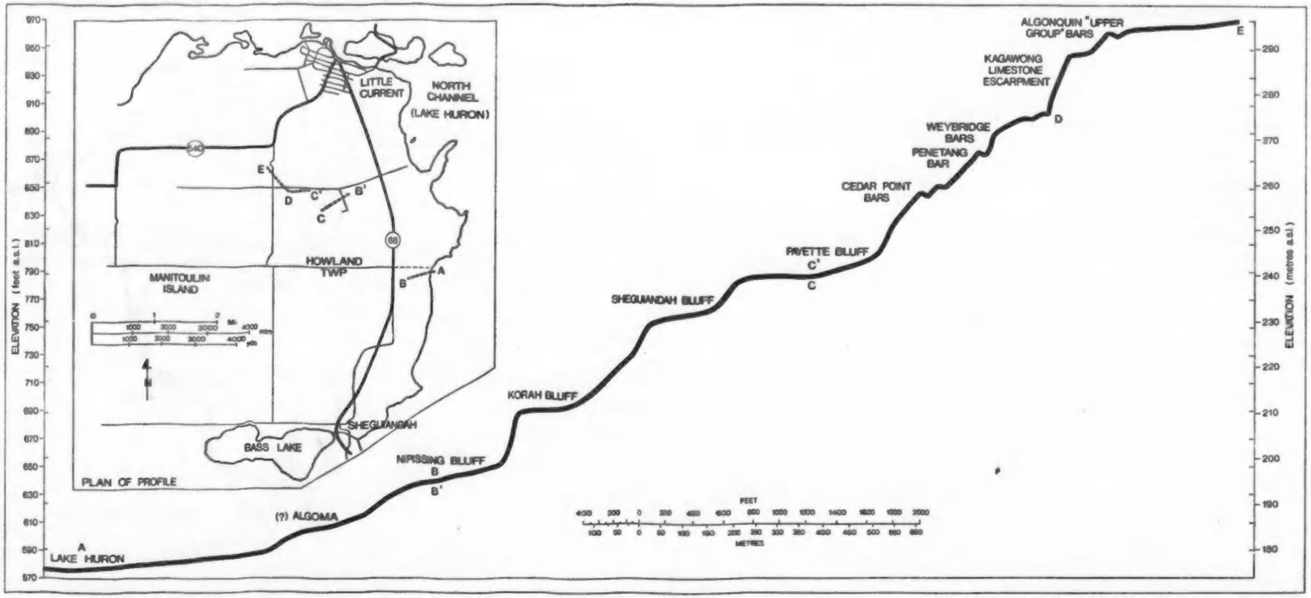


FIG. 10. East to west profile of post-Algonquin shorelines on Manitoulin Island, 3 km south of Little Current, Ont.

basins is significantly lower than observed in Michigan and Ontario basins.

It should be noted that subaqueous erosion and nondepositional environments typify much of the immediately offshore zones of the deeper lakes, where upwelling and longshore current activities are persistent.

Rates of Sedimentation

Kemp et al. (1973) recently summarized results of core analyses from lakes Ontario, Erie, and Huron. Cores were taken from representative areas of fine-grained sediment accumulating in the depositional basins of the lakes. Time horizons were established by pollen analysis using the Ambrosia (ragweed) pollen rise dated at 1850 and the decline of Castanea (chestnut) pollen dated at 1930 for Lake Ontario and 1935 for Lake Erie. Sedimentation rates were calculated assuming constant sedimentation rates above both time horizons. Annual total sediment loadings were calculated using the surface area of the depositional basins and the rates of accumulation derived from the cores. The results are summarized in Table 1. The annual thicknesses of sediment accumulation are considerably higher than the 0.15 mm/yr given for Lake Superior by Farrand (1969). Kemp et al. (1973) noted a threefold increase in sedimentation rate in Lake Erie and the Kingston Basin of Lake Ontario since the European settlement of the lake drainage basins.

Surficial Sediment Distributions in Relation to Energy Controlled Processes

This chapter is included to provide coverage of a topic of some considerable importance in terms of large-lake limnology. However, it should be pointed out that the following discussion is a synopsis of a more detailed publication, already available (Sly 1973).

INFLUENCE OF SOURCE MATERIAL

Along considerable lengths of Great Lakes shoreline, resistant Precambrian bedrock and Lower Palaeozoic Limestone and Dolomitic series are exposed (Fig. 1 and 2). The contributions of nearshore materials from these sources (derived since effective lake level stabilization about 2000 years BP) may be considered negligible. The most abundant materials in the nearshore zone are derived from areas where reworking of existing sandy deposits or glacial sequences can be effective — typically, along the shorelines of the lower lakes.

TABLE 1. Annual sedimentation rates and loadings in lakes Ontario, Erie, and Huron.

Lake	Basin annual sediment accumulation (*metric tons*)	Range of annual thickness of sediment accumulation (*mm*)
Ontario	4,600,000	1.3–9.6
Erie	23,400,000	3.5–24.0
Huron	3,900,000	0.8–1.9

Data derived from cores (Kemp et al. 1973); large areas of the lakes have zero sedimentation.

Source conditions may affect the sedimentary environment in many other ways. Duane (1967) has shown that the St. Clair–Detroit River system acts as a pipeline for sediment transported southward from Lake Huron, which therefore controls the character of much of the material in the western basin of Lake Erie. Fricbergs (1970), however, in his study of Scarborough Bluffs (Toronto) showed that although 300,000 m^3 of material were being annually eroded, only 19,000 m^3 (6%) of this was incorporated into the longshore drift system. This was because most of this eroded Pleistocene material was too fine to be kept as beach material, and was transported offshore. Similar situations also exist in Lake Erie, where erosion of "soft" glacial and postglacial materials may average 1.0–1.5 m/yr (Great Lakes Levels Board, Shoreline physical characteristics [Canadian Federal Department of Public Works], surveys and unpublished data, Haras).

PROCESS CHANGES WITH TIME

There are four main aspects to time controlled energy-related processes: 1) basin-wide changes in energy levels which are dependent on climatic change, 2) basin-wide changes which are related to differences in water level, 3) basin-wide changes which are related to expansion and shallowing, due to natural erosion-accumulation trends, 4) local changes which affect only part of a basin such as the development of spits and bars, or increased/decreased inflow due to river capture or similar drainage modifications.

Points (1) and (2) have been illustrated in the preceding section.

It is difficult to provide unquestionable data in support of basin-wide changes which are related to infilling and shallowing, etc.; nevertheless, it may be seen that with an estimated sediment accumulation rate of 0.2–0.3 cm/yr in the western basin of Lake Erie (A. L. W. Kemp, personal communication), and shoreline recession rates of up to 1.5 m/yr (previously cited), significant changes could be effected over a water level stand period of, say, 2000 years. An uncorrected first-order estimate might then imply a shallowing of such a basin by 30–35% and a surface area increase of 15–20%.

There are, of course, many examples of local changes, affecting only part of a basin. The development of the Toronto Island area (Lewis and Sly 1971) for instance, has provided an extensive lagoonal area of low wave energy, the growth of which has really only stabilized during the past 80 yr or so under the influence of man-made structures. In eastern Lake Erie, Long Point continues to extend southeastward at a rate of about

7 m/yr and thereby adds another 6–8% to the area of the existing bay, on the north side, in the form of a protected zone, each 100 yr. Berg and Duane (1968) recorded the migration of Presque'isle, a similar feature on the south shore of the lake, at a rate of about 5.5 m/yr, before being artificially reduced.

WAVE ENERGY

Surface waves interact with bottom sediments in two ways: (1) as breaking waves in the beach zone, and (2) in that zone affected by the orbital velocities of water motion (beyond the breaker zone). When considering wave action, therefore, the two zones may be viewed together and, as a generality, wave base (WB) is here defined as that depth corresponding to not less than 25% of the available wave motion.

Table 2 illustrates the percentage area of each lake that lies within wave base, and provides an estimate of significant wave height (H_3) which could be derived from the maximum and cross-lake fetch. With the exception of Lake Erie, it may be seen that the affected zone is about 5% or less in each of the lakes.

In both lakes Ontario and Huron, Thomas et al. (1972) have shown that sand-sized materials are limited to the shallower shoreline and nearshore areas, where they form 32% and 38%, respectively, of the total sediment composition. Such values imply that the occurrence of sand particulates is related to more factors than wave energy alone; although submerged (low lake level phases) sand deposits of nonpenecontemporaneous origin undoubtedly account for much of this variance.

In Lake Ontario, C. Jonys (unpublished data) has shown that about 55% of the sand is contributed by inflowing rivers and streams; of the remaining 45%, however, about 28% must be accounted for by processes other than wave action. This discrepancy is almost certainly made up by the various, subaqueous current associated processes.

In the nearshore, wave action provides most of the "erosional energy" and part of the "transportative energy"; such activities may be separated into processes associated with longshore drift, and onshore–offshore migration. The lack of sands in most deepwater sediments (Fig. 3 and 7) indicates onshore–offshore processes are limited in extent and only rarely provide an escape from what is essentially a closed system in the nearshore.

The response of Great Lakes to longshore drift has been documented by many authors, (Berg and Duane 1968; Rukavina 1969, 1970; and Hands 1970), and there seems to be little doubt that certain well-defined net sediment transport paths have been active since post-Pleistocene times. Bajorunas (1970) studied littoral transport in southern Lake Huron where wave duration was found to be the significant variable if less than about 12 h, while effective shoreline length (20 km) became a critical control for more extended periods. Dimensional analysis indicated that transport rates increased with the square root of the sediment size. It was also found that the theoretical equations (e.g. material transport — $(KH^2L \cos \alpha)/8$ [Bascom 1964]) which utilized wave energy, angle of approach, and shoreline length, could give a reasonable estimate of sediment movement if wind, waves, and currents held the same general direction. However, in the complex environment of the nearshore, such estimates could fail; in such cases current speed and direction became the determining factor. In this regard Saylor (1966) showed that wind-generated currents could reach equilibrium with the wind at about 0.033 of the wind speed. This occurred rather quickly (1–3 h), and such currents could persist for days after wind cessation. Currents in the open lake flowed 10–15° to the right of the wind direction, with current speed and direction almost independent of surface wave action. Local variations in the shoreline frequently caused currents and waves to oppose, and under such conditions the data showed a strong correlation between sediment transport and current speed. There appeared to be no upper limit to this relation.

As an example of this latter point, Freeman et al. (1972) discussed the effects of a severe storm surge at Sarnia, also in southern Lake Huron, during August 1971. During this storm approximately 60,000 m³ of sandy material were eroded, but only about 25,000 m³ were later redeposited on shore; the remainder was almost certainly transported southwards, likely by a persistent longshore current having a continuing velocity in excess of 1000 m/h (28 cm/s).

TABLE 2. Wave influence on Great Lake sediments, generalized.

Lake	Max fetch (*km*)	H_3(*m*)	WB 25% (*m*)	Cross fetch (*km*)	H_3(*m*)	WB 25% (*m*)	% affected
Superior	580	7–8	58	250	4	33	5
Michigan	420	6	46	95	1.5–2.0	17	5
Huron	350	5	42	160	2.5–3.0	23	5
Georgian Bay	200	3.5–4.0	28	70	1.0–1.5	12	5
Erie	340	5	42	90	1.5–2.0	17	20
Ontario	290	4.0–4.5	37	75	1.5	12	5

(After Sly 1973)

Studies on onshore/offshore sediment migrations in the Great Lakes have been much less well developed than those of longshore drift. Cook (1970) made a comment on this type of response by lacustrine beaches: "Certain differences seem to exist in the hydrodynamic regimes of high and low energy shorelines. While directional inequalities in wave-induced oscillations are not pronounced in the nearshore zone of an ocean beach, shoreward surges are notably dominant in lakes or wave tanks. Also, rip currents are not well developed along low energy beaches, and water may return offshore by other means. These disparities cast doubt on the applicability of sand transport models for oceanic coasts to protected lacustrine shores." Lewis and Sly (1971), in their study off Toronto, suggested there might be grounds for supporting the null-point theory (Miller and Zeigler 1964); this could be expected where such environments remained uninfluenced by tidal processes.

CIRCULATION AND FLOW

The observed long-term water movements appear to be largely geostrophic, but with modification by persistent (and occasional) baroclinic circulation (e.g. Lake Michigan and southern Lake Ontario), and the influence of continuing large scale inflows such as the Detroit River (Lake Erie) and Niagara River (Lake Ontario).

Geostrophic circulations have generally low velocities of a few centimetres per second; they also show less velocity difference with depth. Baroclinic circulations have much higher velocities (Csanady and Pade 1968, 1969; Scott et al. 1971) of up to 50 cm/s or more at or near surface; near Oswego (Lake Ontario), such currents have been observed in a band 4–8 km offshore and to a depth of 35 m. The mean daily mass transport of such currents was estimated at about 2.4 km^3/day, with a maximum probably in excess of 5 km^3/day; for comparison this is 4 to 6 times greater than the average inflow of the Niagara River at a comparable time. Studies on barotropic circulation show that similar high values may also occur.

Seiches are of importance in all of the Great Lakes, and maximum ranges of from 2.56 m in Lake Erie to 0.76 m in Lake Huron have been recorded (McDonald 1954). Oscillation periods in Lake Erie are from 14 to 16 h, and for Lake Ontario slightly less. Seiches in the Great Lakes respond mostly to wind stress.

Upwelling circulation is common and has been observed throughout the year. Lee (1972) discussed aspects of available data with regard to Lake Ontario, and Burns and Ross (1972) similarly discussed Lake Erie data. Generally, epilimnion flow exceeds hypolimnion flow by an order of magnitude; however, in Lake Erie short period epilimnion maximum flows have been recorded in excess of 75 cm/s, and hypolimnion flows of more than 95 cm/s have also been measured.

The significance of river inflow has already been mentioned; in this respect, it is interesting to note that the total discharge of the Niagara River averages about 5500 m^3/s and ranges between 80 cm/s and 300 cm/s, and may be generalized at about 100 cm/s. The inflow is significant in maintaining an easterly flow along the south shore of the lake, and the extent and influence of this river inflow has been clearly demonstrated by Simons and Jordan (1972).

SEDIMENT RESPONSE TO CIRCULATORY PROCESSES

It is impractical at present to try to correlate sediment distributions with specific geostrophic, baroclinic, or barotropic regimes, etc.; from existing information, however, examples of "preferred" relations can be given.

McAndrews (1972) discussed the presence of pollen in Lake Ontario sediments and the correlation between unique point sources (Black River) and general lake circulation. It seems that fine particulates from the Black River enter the main basin of the lake and are distributed in a manner probably reflecting a geostrophic gyre.

The computed circulations of Simons and Jordan (1972) have also been compared with the distribution of silt and clay size fractions in the deeper waters of Lake Ontario, as described by Thomas (1969) and Thomas et al. (1972). The circulatory "cells" in the main basin bear a striking resemblance to the three sedimentological sub-basins. In addition (R. L. Thomas, unpublished data), there is strong evidence from the distribution and composition of bottom sediments to suggest the incorporation of Niagara River derived materials in the anticlockwise movement of Simons' and Jordan's most westerly "circulatory cell."

In Lake Erie, Hartley (1968) and Burns and Ross (1972) demonstrated the persistence of northerly cross lake bottom currents, particularly in the area east of Point Pelee. A corresponding association has been established with the fine bottom sediments, and C. F. M. Lewis (personal communications, and unpublished data) has evidence for the continuing dispersal of fines in the form of extending bottom deposits.

Seiches, as such, have little effect on bottom deposits, although the storm activity with which they are frequently associated induces severe turbulence and wave action. Rather, they provide a means of further extending the transportive capacity of local current and circulatory regimes, and may account for the presence of coarser sediment deposits beyond the range of normal depositional conditions (P. G. Sly, personal observations).

Numerous authors (Ayers and Hough 1964; Gross et al. 1970; Kennedy et al. 1971; Linebach et al. 1970; Shimp et al. 1971; Gross et al. 1972; and St. John et al. 1972) have discussed the general implications of sediment geochemical parameters in relation to source and circulation, typically geostrophic and kinetic processes. This topic is considered in more detail in the succeeding chapters.

TOTAL ENERGY RELATIONS

By using the data of Thomas et al. (1972, 1973) on the distribution of sediments in lakes Ontario and

Huron, the data of Seibold (1967) and Seibold et al. (1971) relating to the Baltic Sea, the data of Pelletier (1968) on Hudson Bay, and that of Sly (1966) on the sediment distributions in Liverpool Bay, a rough "order of magnitude" comparison may be made on sediment energy levels of such differing environments. It may be seen that the total sediment energy level of the nearshore environment of the Great Lakes is considerably lower than that observed in open marine conditions and it is also lower than that observed in restricted marine conditions (such as Hudson Bay); it is most comparable to the Baltic Sea. The extremes are illustrated by the sand: silt and clay ratios; Liverpool Bay 14.1:1, Lake Huron 1.69:1, and Lake Ontario 1.39:1.

Pelletier (1972) considered such relations further and considered that the silt:clay ratio may be additionally diagnostic of low energy environments.

The significance of such a relation has not been explored; further, it would likely be unsuitable for cross-correlation beyond the freshwater environment because of the influence of flocculation.

OTHER SEDIMENT–ENERGY RELATIONS

The occurrence of density flows (for example river inflows having a different temperature to that of the surrounding lake water) have been well documented from many points of the Great Lakes and, during spring runoff and early summer, the discreet transport of sediment burdened water, as a density flow, is a common feature. Many examples of density flows have been quoted in the literature, perhaps the most applicable being that of Anderson and Pritchard (1951), which relates to density flows in Lake Mead, and that of Forel (1895) and Dussart (1948) on Lake Geneva. In the Great Lakes, however, little work has been undertaken to relate the evidence of sediment distribution to such phenomena, although such relations are known to exist.

The existence of a turbidite type sediment has been recorded by Hough (1963), in Lake Michigan, and no doubt similar deposits exist in other areas of the Great Lakes, but have so far escaped detection.

Lewis and Sly (1971) discussed the possible origin of some sediment deposits offshore from Toronto, where seismic data suggests that slope instability may have given rise to slumping; similar structures, also, have been noted off the Niagara River (P. G. Sly, personal observation). Evidence for sediment slumping in the deeper parts of Georgian Bay and Lake Huron may also be found on many echo traces, though the question arises as to whether such movements are in response to an unstable morphology, or to some form of current-induced shear.

Lewis and Sly (1971) also commented on the possible origin of some recent thin sediment accumulations off Toronto. It has been proposed that these anomalous deposits may reflect the existence of a natural "dumping zone" at the "vertical" interface between more rapidly moving nearshore circulation and that of the slower deep-water basin regime. It is impossible at present to further substantiate such a hypothesis, but no doubt other situations such as the existence of thermal bars (Rodgers 1968) could provide a similar circumstance.

The influence of convection currents on sediment distributions in large lakes has not, to the authors' knowledge, been considered in the Great Lakes. However, the work of Gould and Budinger (1958) suggested that this may be a further aspect of sediment-energy relations which should be considered.

Recent Sediment Geochemistry of the Great Lakes

In recent sediments, geochemical studies have been aimed at low temperature process chemistry and the regional description and quantification of the elements in specific environments. Many detailed studies of both topics have been undertaken in the marine environment and these have formed the basis of our current understanding. Unfortunately, little detailed work has been undertaken in the lacustrine environment, and that available has been confined to small lakes (e.g. Mortimer 1941; Cowgill and Hutchinson 1970). Our knowledge of large lake geochemical processes, in particular the Laurentian Great Lakes, is extremely scanty and indeed no elemental base level compositions have been established.

A review of work on the chemical composition of the bottom sediments of the Great Lakes, at this time, is therefore extremely limited and is concerned predominantly with those elements that have been subjected to more detailed investigations.

MAJOR ELEMENTS AND THE INFLUENCE OF TEXTURAL CHARACTERISTICS

A limited number of studies have been published on the major element geochemistry of the Great Lakes. The most detailed have been carried out in Lake Superior by Nussmann (1965), lakes Superior and Michigan by Callender (1969), and in southern Lake Michigan by Shimp et al. (1970). No significant interpretations were made on major elements in these studies, though Nussmann suggested that SIO_2 related to quartz content. Callender suggested that CaO and MgO in the solid phase of the sediments of lakes Michigan and Superior reflected the concentrations of calcite and dolomite.

The primary use of major element analyses in sediment geochemistry is to indicate the predominant mineral phases present. This in turn may provide some insight into sediment dispersal, and form a mineralogical base for the interpretation of the manner in which trace metals and other components (for example pesticides) may be bound in the sediment. A knowledge of the major element composition is thus fundamental to a realistic interpretation of geochemical and, in some cases, physical processes in a lake system.

The bulk mineralogical compositions of the sediments of lakes Ontario and Huron include quartz, feldspar, clay, carbonate, organic matter, hydrated oxides of iron, and manganese and sulphide, the diagnostic major elements of which are given in Table 3. In addition, Table 3 outlines the relation of the major elements to the texture of the sediment defined in terms of sand, silt, and clay (Thomas et al. 1972, 1973).

Detrital quartz and feldspar (Table 3) are combined due to the fact that a separation of these mineral forms was not possible by the gravimetric procedure used (Trostell and Wynne 1940). Thomas (1969b) was able to characterize the feldspars in Lake Ontario sediments by chemical fractionation and determination of K, Na, and Ca as end-member cations in the isomorphous orthoclase and plagioclase series. The regional distribution of cation ratios in the lake gave evidence of the chemical resistance of the feldspars to transportation and demonstrated an increase in resistance, orthoclase relative to plagioclase, outwards into the central basin regions of the lake. Total K_2O and CaO do not show any relationships to the detrital feldspars, due to masking by the contribution from the clays and carbonates, respectively. Both Na_2O and SiO_2 show positive relations to the sand content, agreeing with the interpretation of Nussmann (1965) for the predominantly detrital origin of these elements in the form of quartz and feldspar.

Clay concentrations are indicated by Al_2O_3 and TiO_2. In Lake Ontario, the degree of relation of TiO_2 to the clay size fraction, for all lake samples, is lower than that indicated for Lake Huron (Table 3). This is due to the fact that in nearshore sediments TiO_2 shows a good correlation with total iron, indicating the presence of ilmenite and/or rutile, whereas in the fine offshore sediments TiO_2 is held by the clays (R. L. Thomas, unpublished data). The clay minerals in the sediments of both lakes Huron and Ontario consist predominantly of illite and chlorite, which is reflected by the relation of K_2O and MgO to the clay size fraction.

In the sediments of both lakes CaO is held predominantly in the form of calcium carbonate. It is interesting to note that the carbonate (indicated by inorganic carbon, Table 3) is contained predominantly in the silt-size fraction of the sediment. This silt-size carbonate has had a modifying effect on the grain-size distribution curves for the sediment samples of the Great Lakes, as has been discussed in some detail by Thomas et al. (1972, 1973).

Organic matter (Org. C) shows a strong affinity for the silt and clay-size fractions. This has been discussed

TABLE 3. Major element relationships in Great Lakes sediments. (Values given are correlation coefficients derived from regression analysis.)

Mineral phase	Major element	Degree of textural relation Sand r[a]	Silt r[a]	Clay r[a]	Lake
Detrital quartz	SiO_2)	.869	–	–	Ontario
and Feldspar	Na_2O (Albitic))	.850	–	–	Huron
Clays	Al_2O_3	–	–	.799	Ontario
		–	–	.895	Huron
Illite	TiO_2	–	–	.468	Ontario
		–	–	.843	Huron
	K_2O	–	–	.756	Ontario
		–	–	.904	Huron
Chlorite	MgO				Ontario
					Huron
Carbonate	CaO	–	.299	–	Ontario
		–	.407	–	Huron
	Inorganic C	–	.443	–	Ontario
		–	.428	–	Huron
Sulphides	S	–	.577	.558	Ontario
		–	.566	.586	Huron
Organic matter	Organic C	–	.504	.759	Ontario
		–	.638	.661	Huron
Hydrated oxides	Fe_2O_3	–	–	.743	Ontario
		–	–	.911	Huron
	MnO	–	–	.221	Ontario
		–	–	.427	Huron
	P_2O_5	–	–	.681	Ontario
		–	.632	.645	Huron

[a] r — Correlation coefficient derived from linear regression analysis.

by Kemp (1969) and Thomas (1969a). The geochemistry of sulphur in the sediments of the Great Lakes has not been studied in detail. Sulphides are an obvious constituent of the deeper reducing muds of the Great Lakes, but it is likely that much of the total S may be organic bound, as suggested by Shimp et al. (1970) for southern Lake Michigan. A high degree of correlation of S to Org. C has been observed in lakes Ontario and Huron (Thomas 1972, 1973), and it is probable that the sulphur is held both as iron sulphide and with the organic matter.

In lakes Ontario and Huron, total Fe_2O_3 shows a strong relation with Al_2O_3 (r = .826 and .941, respectively). This agrees with data reported from Wisconsin lakes by Williams et al. (1971) and from Lake Geneva by Vernet and Thomas (1972). It was suggested by the latter authors, and by Thomas (1973), that the iron is predominantly in the form of hydrated iron oxide with complexed inorganic phosphorus occurring as coatings on individual clay particles (Carroll 1958).

The relation of sediment texture to mean circulation energy in lake systems has been discussed previously. It can also be seen from the brief discussion on major elements that these elements are bound in discreet mineral phases which show strong relations with sediment texture defined by percentage sand, silt, and clay. Thomas et al. (1972, 1973) in studies of sediment texture suggested that the size characteristics of the sediments of lakes Ontario and Huron could be interpreted on the basis of a mixing of two sediment populations, sand and clay. The degree of mixing of the populations, relative to circulation energy, controls the textural characteristics of the sediment at its point of deposition. The relations of the major elements to the sand and clay populations suggests that they can be defined in terms of mineralogy as well as by grain size. Variation in circulation energy thus leads to separation of the inert detrital quartz and feldspars from the geochemically active clays and associated hydrated oxides and organic matter. The potential of the lake sediments in relation to the uptake and release of nutrients, trace elements, and toxic compounds, is thus intimately related to the physical and sediment textural characteristics of the individual lake. No realistic interpretation of geochemical interactions in a lake system can therefore be undertaken without an assessment of the sedimentological processes involved and the utilization of major element distribution as an indicator of the mineral phases present.

TRACE ELEMENTS

Little has been published on the trace element geochemistry of the sediments of the Great Lakes. The most detailed studies have been carried out in Lake Superior by Nussmann (1956) and in southern Lake Michigan by workers of the Illinois State Survey (Kennedy et al. 1971; Shimp et al. 1970, 1971). More restricted trace element studies on the sediments of Lake Superior have been reported in relation to mineralization on the Keweenaw Peninsula by Moore et al. (1972) and Smith and Moore (1972). Potter et al. (1963) determined trace elements in three sediment samples from Lake Michigan, Kleerekoper (1961) studied strontium in Lake Huron and Lake Erie sediments, and Swain and Prokovich (1957) examined manganese and titanium in sediments off the Silver Bay area of Lake Superior. This conspicuous lack of general trace element information on the sediments of the Great Lakes is temporary as considerable information has been gathered now by a number of agencies, in particular the Canada Centre for Inland Waters. Due to the limited amount of published data, the authors do not intend to undertake a detailed discussion at this time. The information available cannot be considered to be typical of even individual lakes, let alone representative of the entire Great Lakes system. This being the case, the authors have chosen to review the distributions and concentrations of mercury, which may be taken as an example and as a trace element that has been studied in reasonable detail.

MERCURY

The discovery that fish in Lake St. Clair were contaminated by mercury in excess of the 0.5 ppm maximum level in 1969, led to a number of studies to determine the levels of mercury in the bottom sediments of the Great Lakes. The experimental evidence accumulated by Jenson and Jeralov (1969) and Wood et al. (1968) on the microbial methylation of mercury and its almost quantitative transfer to the biota, demonstrated the fundamental importance of residual mercury in the bottom sediments of industrially contaminated lakes. The concentrations of mercury and its distribution in the bottom sediments has been published for lakes Ontario and Huron by Thomas (1972, 1973) and for southern Lake Michigan by Kennedy et al. (1971). The latter authors also showed the vertical variation of mercury with sediment depth in Lake Michigan. Similar though more detailed core profiles have been given for lakes Ontario, Erie, and Huron by Kemp et al. (1973).

The mean concentrations in the surficial sediments of the Great Lakes, where analyzed to date, are given in Table 4. It can be seen that lakes St. Clair, Erie, and Ontario have mercury levels approximately three times those observed in lakes Huron and southern Michigan. Kennedy et al. (1971) noted an increased accumulation of mercury in the uppermost sediment layers of the cores from southern Michigan (range 30–380 ppb). They further noted a relation of the mercury with organic carbon and sulphur, but did not give any explanation for the observed increase. Thomas (1973), in describing mercury distribution in Lake Huron, presented evidence for mercury contamination of the sediments of the southern part of the lake, which he ascribed to input from Saginaw Bay. Based on the published evidence, it appears that some mercury contamination of lakes Michigan and Huron has taken place, and it is evident from the values given for lakes St. Clair, Erie, and Ontario (Table 4) that these lower lakes have suffered even more severe contamination from industrial input. This has been further corroborated by Kemp et al. (1973) who gave annual mercury loadings of 12.7, 17.4, and 1.4 metric tons to the sediments of lakes Ontario, Erie, and Huron respectively.

The distributions of total mercury in the surface sediments of Lake St. Clair and Lake Erie are given in Fig. 11 and 12. In Lake St. Clair (Fig. 11) it can be seen that the highest levels of mercury occur in a line from the St. Clair River to the Detroit River and also in the central deeper water region. The interpretation is that this distribution (Thomas, in preparation) is related to source and to the sediment distribution, and indicates that much of the mercury-enriched sediment is derived from the St. Clair River and is carried directly into the Detroit River, but with some accumulation associated with fine-grain sediment in the deeper water part of the lake. Sediment cores taken in the central part of Lake St. Clair in 1970 showed that modern sediment accumulation is in the order of 14 cm, with mercury enrichment in the topmost 2 cm. This would indicate that the sediments of the lake

TABLE 4. Surface sediment mercury concentrations.

Lake	No. samples	Depth of sample *cm*	Mercury concentration Min ppb	Max ppb	Mean ppb	SD ppb	Source
Ontario	248	0–3	32	2100	651	507	Thomas (1972)
Erie	243	0–3	13	7488	609	703	Thomas (in preparation)
St. Clair	55	0–2	70	2655	632	628	Thomas (in preparation)
Huron	163	0–3	54	805	222	162	Thomas (1973)
S. Michigan	31	Variable[a]	30	380	146	-	Kennedy et al. (1971)

[a] Hg values taken for the topmost sub-samples of the sediment cores. This subsample varied from 1 to 5 cm but was generally the top 2 or 3 cm.

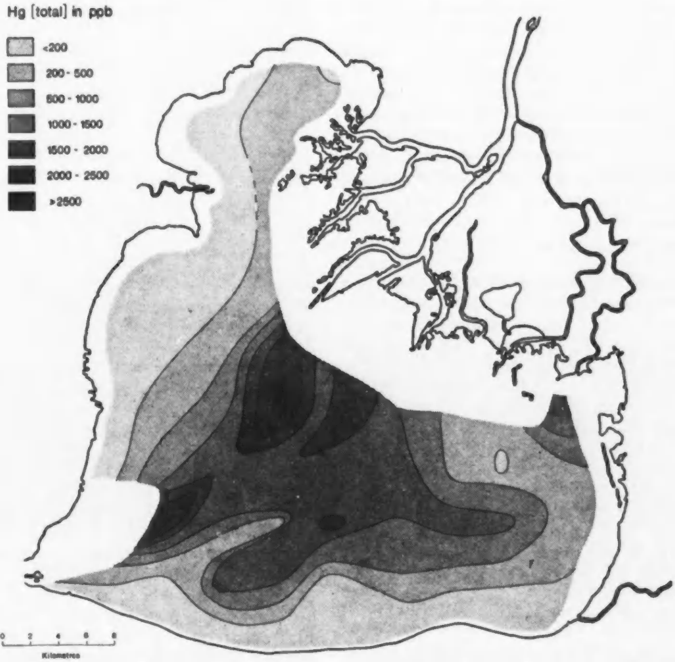


FIG. 11. Distribution of total mercury in the surface sediments of Lake St. Clair.

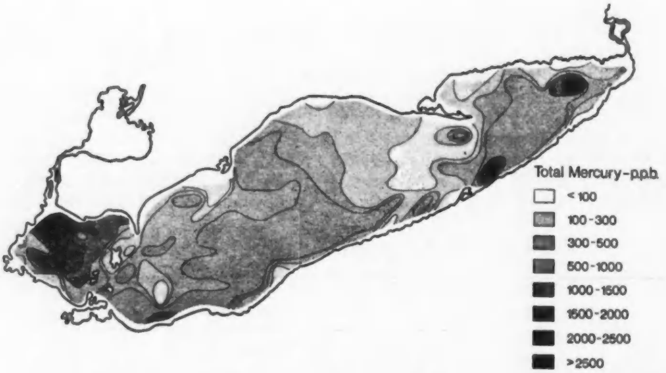


FIG. 12. Distribution of total mercury in the surface sediments of Lake Erie.

are transitory, with the upper sediments available for resuspension during storm weather periods and ultimate transport to the Detroit River.

Figure 12 shows the distribution of total mercury in the sediments of Lake Erie. The distribution is not complex and concentration gradients indicate that the Detroit River is the primary source of mercury to the western basin of the lake. Both the concentrations and distribution of mercury in the western basin of Lake Erie agree well with the data presented by Kovacik and Walter (1973); these authors related mercury distribution to current circulation in the western basin and also noted the Detroit River as the input source. Mercury levels decreased eastwards into the central basin, but persistent concentrations suggest movement along the south shore towards the Niagara River. Additional high values also occur in the eastern basin which may indicate additional inputs to this part of the lake.

FERROMANGANESE CONCRETIONS

The occurrence of freshwater ferromanganese concretions has been well known for many years (for example, Kindle 1932), yet such concretions were not recognized in the Great Lakes until 1968 (Rossman and Callender 1968, 1969), when major concentrations were found in Green Bay and Little Traverse Bay in Lake Michigan. Subsequent finds by Cronan and Thomas (1970) and Damiani et al. (1973) illustrate the extensive nature of these deposits in the Great Lakes.

A number of factors involving the occurrence, composition, and origin of ferromanganese concretions are of considerable value in the understanding of lacustrine physical and chemical processes. Under certain circumstances, they may indicate the trophic state of a lake. They also play a significant role in the geochemical cycles of nutrients Fe, Mn, P, and in the uptake and release of trace metals.

Mode of Occurrence — In the Great Lakes, ferromanganese concretions occur as discrete nodular concretions (Fig. 13), as thin coatings on sand particles and as encrustations on pebbles, cobbles, and boulders. These encrustations occur normally as a ring around the basal part of the cobble, pebble, etc., apparently at the point at which it sits in the lake bed. At all locations observed, the material underlying these parent gravels has proven to be glacial clay. The coated sands, as described in Lake Ontario by Cronan and Thomas (1970, 1972), overlie glacial clays, tills, and glaciolacustrine clays (Thomas et al. 1972). Discrete nodules have been observed occurring on erosional surfaces of glaciolacustrine clays (Fig. 13b) and in association with gravel and sand over glacial clays. Figure 13c shows a glaciolacustrine clay surface taken from the Kingston Basin, Lake Ontario, having a distinct "potholed" appearance. The "potholes" are interpreted as being the result of dissolution of ferromanganese nodules related to changing trophic conditions in this part of the lake.

The occurrence of ferromanganese nodules, and ferromanganese-coated sands in the Great Lakes is given in Fig. 14, which also includes the distribution of an iron and iron with manganese layer in the mud sediments of the lakes discussed later.

The major nodule accumulations occur in Lake Michigan and in the Bay of Quinte, Lake Ontario (Bay of Quinte, Glenora, and Brothers' Island nodules). Ferromanganese-coated sands are extensive on the north slope of Lake Ontario and in Lake Huron northwest of Saginaw Bay. No concretions were observed in Lake Superior and only sparse nodule occurrences were recorded in Lake Erie. The Lake Erie nodules displayed a general pitted conditions which suggested they are residual and not forming at the present time.

The common denominator for all the ferromanganese concretion occurrences, including those in the Bay of Quinte (Damiani et al. 1973), is the fact that they are associated with lag gravel and sand deposits or they occur on surfaces swept clear of sediment. This implies continuous strong circulation, which firstly prohibits sediment deposition and secondly ensures a constant replenishment of soluble iron and manganese required for continued precipitation.

Mode of Formation — The mode of formation of ferromanganese concretions has been a subject of some debate over the years in both marine (Price 1967) and lacustrine (Harris and Troup 1969) environments. The discussion here is concerned only with the occurrences in the Great Lakes, and as such is specifically related to an interpretation of these conditions only. Work to date, however, has not recognized the possible role of bacteria in the formation of the ferromanganese concretions (Perfil'ev et al. 1965). As has been the general practice, the mechanism of formation considered is based on physical and chemical interpretations of origin, which can be related to two major factors. Firstly, the supply of the primary constituents and secondly, the chemical conditions at the point of precipitation (which is believed to exert a fundamental control over the final chemical composition of the concretion).

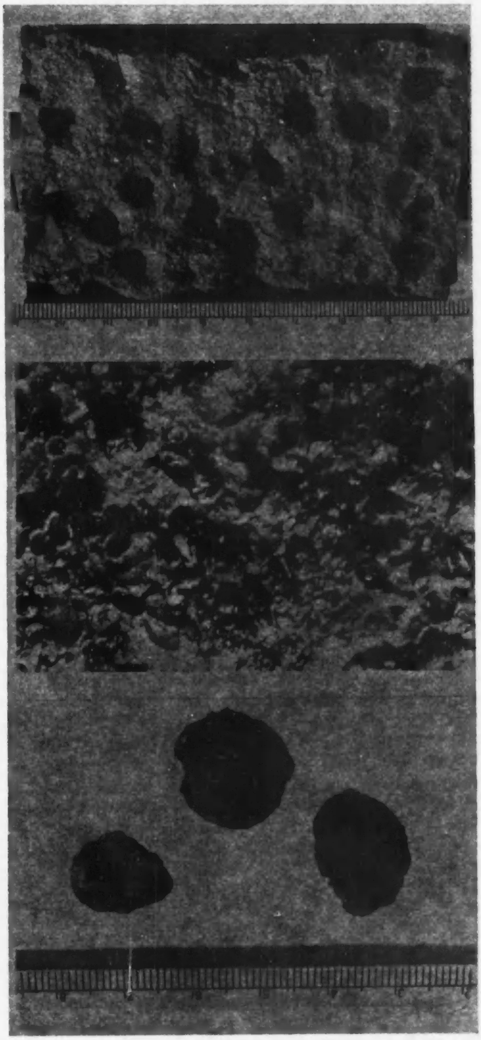


FIG. 13. (*Top*) Ferromanganese nodules from the Big Bay section of the Bay of Quinte, Lake Ontario. (*Center*) Ferromanganese nodules on a glaciolacustrine clay surface, Brothers' Island, Lake Ontario. (*Bottom*) "Potholed" glaciolacustrine clay surface formed by the dissolution of ferromanganese nodules.

Rossman and Callender (1969), in investigating the Fe.Mn composition of interstitial waters in sediment cores underlying the nodule occurrences in Green Bay, observed that these elements were elevated at depth in the cores. This led them to suggest the upward diffusion of Fe and Mn, with subsequent precipitation at the sediment/water interface, as being the mode of origin of these particular concretions. This mechanism has also been suggested for the origin of shallow-water marine nodules by Price (1967). Cronan and Thomas (1972) in their investigation of the Lake Ontario Fe.Mn-coated sands also analyzed interstitial waters, and found increased concentrations of these elements in the upper parts of the core. They concluded that in the regions where the sands overlaid glaciolacustrine clays, upward diffusion may bring about a significant contribution of Fe and Mn. In the regions overlying glacial tills, this mechanism was precluded as a source of the major components, and it was suggested that the elemental source lay in the deepwater muds to the south of the deposit. Harris and Troup (1969), suggested the seasonal mobilization and precipitation of iron and manganese from the deeper water central areas of small lakes, with precipitation around the margins, as it might relate to the seasonal cycle of biologic production and oxygen depletion during stratification in the deeper water areas. This mechanism when transcribed into Great Lakes conditions appears to be, on the basis of available information, the most probable process for the generation of these ferromanganese deposits.

Studies of the hypolimnic waters of Lake Erie (Burns and Ross 1972) have shown the sequential release of Mn, P, and Fe during deoxygenation of bottom waters under conditions of summer stratification. Enrichment of bottom waters with Fe, Mn, and Zn has also been demonstrated in Lake Ontario (Chau et al. 1970), and it was suggested by Cronan and Thomas (1972) that the Lake Ontario deposits were formed by precipitation from these bottom waters during their circulation across the northern slope of the lake. Variation of the Fe:Mn ratio from south to north across the deposit suggested the sequential precipitation of iron, followed by manganese (relative to increasing redox potential into the shallower waters of the coastal zone). This is in agreement with the concept of separation of these elements in the secondary environment, relative to increasing Eh and pH as suggested by Krauskopf (1957).

Detailed visual examinations of sediment grab samples and cores from lakes Ontario, Huron, and Superior (R. L. Thomas, unpublished data) have revealed the presence of a hard limonitic layer at a depth of 2–5 cm in many of the samples. In the fine-grained basin sediments of Lake Superior this crust was observed in all samples, excluding the southwest basin (Duluth Basin, Fig. 4), and consisted of a brown, iron-rich lower layer, overlain by a black manganese-rich layer. This layering is interpreted as being the result of sequential precipitation of iron followed by manganese, derived by upward diffusion from the more reducing deeper horizons of the sediments. Similar iron, and occasionally ironmanganese, layers were observed in parts of Lake Huron and Lake Ontario, but were recorded in only six samples in Lake Erie (Fig. 14). In lakes Huron and Ontario, the Fe layers occurred in basin muds on the outer margins of the basin deposits and were not seen in the central basin regions.

Measurement of Eh values at a sediment depth of 1.5 cm (Thomas et al. 1972, 1973) have shown a gradient of decreasing Eh values from the shallow-water nearshore zones into the deepwater basins in both lakes Ontario and Huron, whereas in Lake Superior the surface sediments have a high redox potential throughout. In Lake Superior it is concluded that Fe and Mn are not released to the bottom waters, which explains the failure to locate manganese nodules during a 1973 regional survey (R. L. Thomas et al. unpublished data). In lakes Huron and Ontario, Fe and Mn are released from the deep water-basin muds, but are retained in the sediments in the peripheral basin region where the redox potential is more positive. This deep water source of Fe and Mn is thus considered to be the primary source of these elements, which are subsequently precipitated as nodules and sand coatings in the more oxidizing but nondepositional, shallower water regions.

Iron oxide layers were rare in Lake Erie, suggesting that the low redox conditions in this lake release all of the available Fe and Mn from the sediments to the hypolimnion (Burns and Ross 1972). It should also be noted that the ferrous iron released is in excess of that required to combine with available sulphide present in the sediment as a product of the microbial reduction of SO_4. During a 1971 sediment survey of Lake Erie, nodules were found at a few locations associated with the lag deposits south of Point Pelee and the north shore. These nodules, however, were sparse and appeared to be residual. It seems, therefore, that present-day conditions in this lake are such that the active formation of ferromanganese deposits is not taking place, even though an abundant supply of primary constituents is available.

In summary, three conditions can be recognized in the Great Lakes which relate to ferromanganese

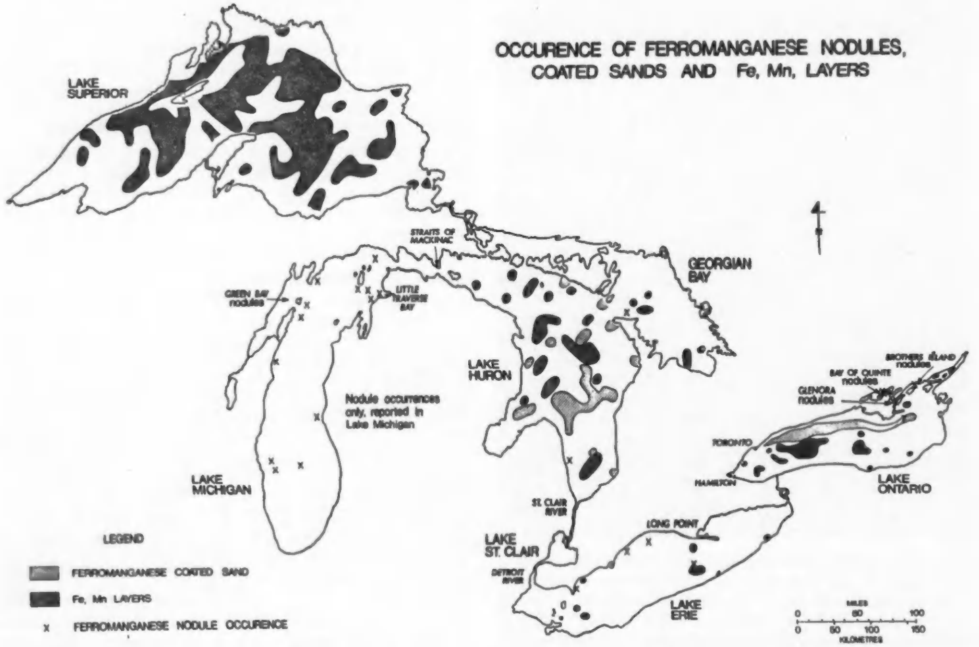

OCCURENCE OF FERROMANGANESE NODULES, COATED SANDS AND Fe, Mn, LAYERS
LAKE SUPERIOR
STRAITS OF MACKINAC
GEORGIAN BAY
GREEN BAY nodules
LITTLE TRAVERSE BAY
LAKE HURON
Nodule occurrences only, reported in Lake Michigan
LAKE MICHIGAN
BROTHERS ISLAND nodules
BAY OF QUINTE nodules
GLENORA nodules
TORONTO
HAMILTON
LAKE ONTARIO
ST. CLAIR RIVER
LONG POINT
LAKE ST. CLAIR
DETROIT RIVER
LAKE ERIE
LEGEND
▨ FERROMANGANESE COATED SAND
■ Fe, Mn LAYERS
x FERROMANGANESE NODULE OCCURENCE
MILES 0 50 100
0 50 100 150 KILOMETRES

FIG. 14. Occurrence of ferromanganese nodules, coated sands, and iron/manganese layers in the Great Lakes.

deposits, and which, in turn, may well be related to the trophic level insofar as such levels are related to the sediment redox potential. Thomas et al. (1972, 1973) have shown statistically that the Eh in lakes Ontario and Huron is related to the organic C concentration, which in turn is partially related to primary productivity. The three conditions can be described as follows:

1) Oxidizing condition, as observed in Lake Superior. Ferromanganese concretions absent or rare due to lack of supply of the primary elements. Deepwater surface sediments are oxidizing (high Eh) which results in the formation of internal layering of Fe and Mn with no release to the hypolimnion. This condition would thus characterize an oligotrophic lake with low biological productivity.
2) Normal condition as characterized by lakes Ontario, Huron, and possibly Michigan. In these lakes, deepwater sediments are higher in organic matter and have lower redox potentials, which result in the release of Mn and Fe from the sediment to the hypolimnion. Shallower-water areas of mud accumulation on the periphery of the basins have an iron or iron manganese layer, as per condition (1) above. Shallower, nondepositional zones of lag deposits with high redox potentials result in the precipitation and accumulation of ferromanganese concretions. It is suggested that such a condition may be characteristic of a late oligotrophic to mesotrophic lake situation.
3) Eutrophic conditions, as observed in Lake Erie. No occurrence of iron layering in the sediment, indicating that the redox conditions of the surface sediments are such that available soluble iron and manganese are released to the hypolimnion. As indicated by the studies of Burns and Ross (1972), this would appear to be a seasonal situation related to oxygen deficiency during summer stratification. Ferromanganese concretions are sparse or absent and indicate that the general redox conditions prohibit the accumulation of deposits in the high-energy zones of the lake. This may be an intermittent phenomena in that some seasonal precipitation may occur, but conditions are insufficiently constant to permit continued uninterrupted growth of the concretions. The presence of some nodules in Lake Erie, probably residual, suggests historically recent deterioration in lake quality. Dissolution of nodules has been observed in the Kingston Basin, as previously noted (Fig. 13c), indicating recent changes in lake conditions in the area.

Composition and Rates of Formation — The chemical composition of ferromanganese concretions from the Great Lakes are given in Table 5. This table includes the composition of four nodules recovered from Lake Erie during 1971, details of which have not been previously reported. Lake Erie nodules show considerable variability in composition in terms of their Fe:Mn ratio which may be due to the wide geographical separation of the localities. The nodules show extreme iron enrichment at locality M-19 to high manganese nodules at J-25 and L-16. In general, it can be seen from Table 5 that Lake Erie nodules are enriched in trace metals, in particular Cd, Cu, Pb, and Zn. In terms of trace metal content they fall between the compositions observed for the Lake Ontario coated sands and the Lake Ontario K-2 nodule.

The enrichment of trace metals in both marine and freshwater nodules is well known, and the scavenging capability of such deposits plays a significant role in the removal of toxic trace metals from the hydrosphere. Conversely, as noted by Edgington and Callender (1969) with particular reference to arsenic, the dissolution of nodules due to changing environmental conditions (eutrophication) might well result in the release of these metals, producing deleterious effects on water quality and the ecosystem.

In terms of mineralogy, no detailed studies have been reported for Great Lakes ferromanganese concretions. Cronan and Thomas (1970) commented on the completely amorphous character of the Lake Ontario coated sands and the K-2 nodule. Damiani et al. (1973) recognized the presence of goethite by X-ray diffraction in iron-rich nodules from the Bay of Quinte, similar to those described by Schoettle and Friedman (1971) from Lake George. In one nodule from the Bay of Quinte, Damiani et al. recorded the first reported occurrence in freshwater nodules of the manganese carbonate rhodochrosite. No other manganese mineral has been reported and, from the evidence to date, it would appear that the Great Lakes nodules rich in manganese are amorphous in character. However, Schoettle and Friedman (1971) noted the occurrence of birnessite in one nodule from Lake George.

The amorphous nature of the deposits described by Cronan and Thomas (1970, 1972) was attributed to the possibility that the concretions are recent in origin, in comparison to their marine counterparts, and thus have had insufficient time to develop crystallinity. No data are available on the absolute rate of formation of the Great Lakes concretions. Schoettle and Friedman (1971), using radiocarbon data analysis,gave an average of 3316 ± 475 yr for a compounded nodule sample from Lake George. Using rate of uplift data, Damiani et al. (1973) gave a maximum age of the Bay of Quinte nodules of 1700–2000 yr. No estimates have yet been made for other nodule occurrences in the lakes, particularly in relation to the large area of the coated-sand deposit in Lake Ontario; such information would be of great value. Assuming constant uplift since the Admiralty Phase of Lake Ontario and knowing the water depths overlying the deposit, the present authors calculate a maximum age for this deposit of 3000–3500 years. The coated sands contain extremely high levels of trace metals, and assuming rapid formation, the removal by dredging of the sands with subsequent regeneration of the deposit might initially appear to be a simple method of removing trace metals from the lake cycle.

To date, no analyses for phosphorus have been reported for the Great Lakes ferromanganese concretions. The known affinity of goethite for phosphorus would indicate that sorbed P may be significant in the deposits.

TABLE 5. Chemical composition of ferromanganese concretions from the Great Lakes.

	Percentage			Fe/Mn Ratio	Parts per million											
	Fe	Mn	Ca		K	Mg	Sr	Be	Cd	Co	Cr	Cu	Pb	Ni	V	Zn
Big Bay S–41	30.24	12.47	1.24	2.43	402	1850	710	2	4	59	37	24	130	26	128	163
Nodules B–1	14.63	10.25	0.95	1.43	3000	6300	765	1	8	112	35	64	70	200	172	201
P–28	40.32	4.50	2.37	8.96	85	757	149	1	5	36	19	16	47	13	90	133
Q–29	40.65	8.65	1.13	4.70	87	600	402	3	5	41	39	18	50	19	122	132
L. Ontario K–2	20.00	20.50	1.30	0.98	2,400	9,000	430	–	–	305	–	90	70	725	–	460
Coated sands	20.53	17.10	3.07	1.20	2,380	21,300	160	–	–	650	–	360	1,890	2,410	–	2,020
L. Michigan Average	20.20	6.10	–	3.31	–	–	–	–	–	200	–	180	–	270	–	320
L. Erie J–25	28.55	16.26	0.82	1.76	10,700	24,600	–	–	25	140	41	353	975	443	–	1,067
M–19	46.76	0.89	6.78	52.54	2,800	61,500	–	–	19	139	63	107	335	394	–	379
L–16	9.36	10.10	1.00	0.93	4,100	22,100	–	–	20	236	84	127	331	510	–	442
G–9	11.79	1.44	2.70	8.19	10,800	46,300	–	–	39	108	40	426	77	448	–	694

CARBON, NITROGEN, AND PHOSPHORUS

Over the past few years a number of studies have been carried out on organic matter in the sediments of the Great Lakes. Lewis and McNeely (1967) found a range of 0.5–5.0% organic carbon in the sediments of Lake Ontario, with concentrations varying with sediment type. Kirk (1962), Robertson and Powers (1968), and Callender (1969) found similar values in lakes Erie, Michigan, and Michigan and Superior respectively. More detailed studies of the spatial and vertical distributions of Org. C (in cores) have been carried out in southern Lake Michigan (Shimp et al. 1971) and in lakes Erie, Ontario, and Huron by Kemp and Lewis (1968), Kemp (1969), and Kemp et al. (1972, 1973).

The major findings of Kemp and co-workers show that the distribution of organic matter in the Great Lakes sediments is related to the clay-size fraction, which in turn co-varies with mean grain size. On the basis of the surface distribution in Lake Huron (Thomas et al. 1973), it was concluded that the southern part of this lake has suffered some trophic deterioration due to the input of nutrients derived from Saginaw Bay. From core data it was concluded that Lake Huron, in general, shows little change over historical time (Kemp et al. 1973). The loadings of organic C, together with nitrogen and phosphorus, to the Lower Great Lakes as indicated by core profiles, shows a progressive increase in the nutrient enrichment of these two lakes (Beeton 1965).

Little detailed work has been undertaken on nitrogen in the sediments of the Great Lakes. The most comprehensive study of nitrogen in surface sediment was carried out by Kemp (1971) on 355 samples from lakes Ontario, Erie, and Huron. Kemp demonstrated that the nitrogen content was directly proportional to the organic carbon content with a carbon–nitrogen ratio ranging from 7 to 13. This work has been further amplified by the analyses of nitrogen in cores taken from the same three lakes (Kemp et al. 1972, 1973).

Phosphorus in the sediments of the Great Lakes has been discussed by a number of authors (Callender 1968; Kemp et al. 1972, 1973; and Williams and Mayer 1972). These publications summarize historical trends in phosphorus loadings and relate the observed levels to the trophic states of the lakes. No authors, as yet, have provided mean phosphorus levels for the sediments of the Great Lakes. The significance of sediment phosphorus, in terms of regeneration to the water column under anaerobic conditions in Lake Erie, has been well demonstrated by Burns and Ross (1972). They calculated that, during 2 mo of oxic and anoxic conditions, 2351 metric tons of phosphorus was regenerated from the sediments compared to a total estimated phosphorus loading of 4071 metric tons.

Preliminary calculations on total phosphorus (as P_2O_5) in the sediments of lakes Ontario, Erie, and Huron give mean values of 0.22, 0.20 and 0.12% dry weight respectively (R. L. Thomas, unpublished data).

The only two phosphate minerals that have been observed in the sediments of the Great Lakes are apatite, probably of detrital origin, and vivianite which has formed authigenically. These have been observed in sediments of lakes Superior, Erie, and Ontario but they probably occur in the other Great Lakes as well (Dell 1973).

Future Trends in Research

Future activities related to limnology in the field of recent geological studies will certainly build on the evidence and interpretations already established. It is clear that many large lake processes are closely allied to those observed on continental margins and that, although comparison may be made with both marine conditions and small freshwater lakes, large lake studies must stand on their own as distinct entities.

It is also clear that studies will continue along at least two strongly related but separately defined pathways: those oriented towards the understanding of natural processes and the complex interactions between the physical, chemical, and biological components of sediment/water interfaces; and those applied towards particular human-related concerns.

It should be indicated that limnological studies have now reached a level of sophistication such that they can begin to incorporate data inputs which relate primarily to such external stimulii as the character of basin inputs and atmospheric loading. Undoubtedly, future geological studies within the Great Lakes must be designed to be more cognizant of such inputs and of the interaction between the water body and its surrounding drainage basin as a whole. The latter point carries an additional impetus, as basin management becomes more effective as a refined approach to resource utilization.

At the present time the following topics are seen as presenting particularly valuable avenues for research; their sequence is not intended to imply a preferred or priority rating: — Detailed investigations of shoreline and nearshore processes to evaluate the relative dominance and overriding control of such factors as the significance of bluff materials (and their engineering properties) and wave action in shore erosion; the influence of ice, both as a protective cover and as an erosional force (through freeze–thaw effects); the significance of onshore–offshore sediment migration in terms of seasonal and long-term changes (and in response to lake level fluctuations); and the mechanisms and quantitative aspects of subaqueous erosion beyond the breaker zone. — The mechanisms, occurrence, and emplacement of density and turbidity "flow" related sediments. — Studies on the significance of internal waves in turbulent mixing zones, as a mechanism for transport of fine particulates. — The concentrations, distributions, and characteristics of the suspended load fractions, observed both within and beyond the nearshore zone, and their physical/chemical and diagenetic responses over seasonal (and longer) time frames. — Investigations of phosphorous concentrations relative to the rates of nodule (and concretionary) formation, and the associated trace metal uptake (removal) mechanisms. — The determination of complete spatial (and selected temporal) distributions and concentrations of trace metals, and an assessment of factors which may influence maximum sediment concentrations. — The assessment of interactions between fine-grained mineral phases and the water column, which may take place under exposure to various turbulent, pH, oxic, or anoxic, and temperature-variable conditions. — The determination of the various forms of trace metals and toxic compounds held in sediments, and an assessment of biogeochemical transfers effected by microbiological populations. — Studies of the various relations which may exist between benthic populations, fish, and sediments. — Detailed investigations on the interactions between sediments and water quality, to assess the role of clay minerals, amorphous hydroxides (iron colloids), and complex particulate organics in the exchange of trace metals and toxic compounds. — The establishment of total sediment-geochemical budgets, and through "interaction modelling" refine those parameters which appear most sensitive as indicators of trophic state.

A further detail of those topics of a more applied nature, must necessarily incorporate understanding of many of the aspects already raised; in such cases it is not so much the gathering of new and additional data, but rather the interpretation of it in the light of applied human objectives: — The evaluation of dredging and dumping of bottom sediments and the treatment or covering of contaminated materials. — The construction of new channels, structures, or otherwise modifying and influencing existing sediment-energy relations. — The preservation and development of wetland areas to support biological communities and to act as a buffer zone between surface runoff and main lake water receipt. — The development of shoreline design, (and perhaps later, of whole basins such as man-made lakes) to ensure optimum conservation and economic shoreline use.

Conclusions

In summarizing the geological studies on recent sediments in the Great Lakes, it is clear that, although much published material is available, considerably more work is necessary to answer the types of problems which have been outlined above. It is proper to point out that many research programs are currently underway which should eventually provide many of the answers. It is anticipated that publications during the next 2–5 yr will provide a strong basis in this respect.

Acknowledgments

The authors would like to express thanks to their many colleagues at the Canada Centre for Inland Waters (CCIW) who so generously provided data and valuable discussion for inclusion in this publication. In particular the assistance of A. L. W. Kemp is gratefully acknowledged.

The Director (CCIW), J. P. Bruce, is acknowledged for permission to publish this material.

Anderson, E. R., and D. W. Pritchard. 1951. Physical limnology of Lake Mead. U.S. Navy Electron. Lab. Rep. 258.

Ayres, J. C., and J. L. Hough. 1964. Studies of water movements and sediments in southern Lake Michigan: Part II. The surficial bottom sediments in 1962–1963. Univ. Mich. Great Lakes Res. Div. Spec. Publ. No. 19.

Bajorunas, L. 1970. Littoral transport and energy relationships, p. 787–798. *In* Proc. 12th Coastal Eng. Conf., Washington, D.C.

Bascom, W. 1964. Waves and beaches — the dynamics of the ocean surface. Doubleday and Co., New York, N.Y. 267 p.

Beeton, A. M. 1965. Eutrophication of the St. Lawrence Great Lakes: Limnol. Oceanogr. 10: 240–254.

Berg, D. W., and D. B. Duane. 1968. Effect of particle size and distribution on stability of artificially filled beach, Presque'isle Peninsula, p. 161–178. *In* Proc. 11th Conf. Great Lakes Res. 1968.

Broecker, W. S., and W. R. Farrand. 1963. Radio carbon age of the Two Creeks Forest bed. Geol. Soc. Am. Bull. 74: 000 p.

Burns, N. M., and C. Ross. 1972. Project Hypo, an intensive study of the Lake Erie central basin hypolimnion and related surface water phenomena. Can. Cent. Inland Waters Pap. No. 6. U.S. Environ. Prot. Agency, Tech. Rep. No. TS-05–71–208–24.

Callender, E. 1969. Geochemical characteristics of Lakes Michigan and Superior sediments, p. 124–160. *In* Proc. 12th Conf. Great Lakes Res. 1969. Int. Assoc. Great Lakes Res.

Carroll, D. 1958. Role of clay minerals in the transportation of iron. Geochim. Cosmochim. Acta. 14: 1–28.

Chau, Y. K., V. K. Chawla, H. F. Nicholson, and R. A. Vollenweider. 1970. Distribution of trace elements and chlorophyll *a* in Lake Ontario, p. 659–672. *In* Proc. 13th Conf. Great Lakes Res. Int. Assoc. Great Lakes Res.

Cook, D. O. 1970. Models for nearshore sand transport, p. 210–216. *In* Proc. 13th Conf. Great Lakes Res. Int. Assoc. Great Lakes Res.

Cowgill, U. M., and G. E. Hutchinson. 1970. Lago DiMonterosi: chemistry and mineralogy of the sediments and their source materials. Trans. Am. Philos. Soc. 60: 37–101.

Cronan, D. S., and R. L. Thomas. 1970. Ferromanganese concretions in Lake Ontario. J. Can. Earth Sci. 7: 1347–1349.

1972. Geochemistry of ferromanganese oxide concretions and associated deposits in Lake Ontario. Am. Geol. Soc. Bull., 83.

Csanady, G. T., and B. Pade. 1968. Coastal jet project. Environ. fluid mech. Lab. Rep. No. 1. Univ. Waterloo, Waterloo, Ont. 000 p.

1969. Coastal jet project. Environ. Fluid Mech. Lab. Rep. No. 2. Univ. Waterloo, Waterloo, Ont.

Damiani, V., T. W. Morton, and R. L. Thomas. 1973. Freshwater ferromanganese nodules from the Big Bay section of the Bay of Quinte, northern

Lake Ontario. *In* Proc. 16th Conf. Great Lakes Res. Int. Assoc. Great Lakes Res. (In press)

Dell, C. I. 1972. The origin and characteristics of Lake Superior sediments, p. 361–370. *In* Proc. 15th Conf. Great Lakes Res. Int. Assoc. Great Lakes Res.

1973. Vivianite: an authigenic phosphate mineral in Great Lakes sediments. *In* Proc. 16th Conf. Great Lakes Res. Int. Assoc. Great Lakes. (In press).

Douglas, R. J. W. 1970. Economic geology report #1, geology and economic minerals of Canada. Dep. Energy, Mines Res., Ottawa. 838 p.

Dreimanis, A. 1969. Late Pleistocene lakes in the Ontario and Erie basins, p. 170–180. *In* Proc. 12th Conf. Great Lakes Res. Int. Assoc. Great Lakes Res.

Dreimanis, A., P. F. Karrow, and J. Terasmae. 1972. Quaternary stratigraphy and geomorphology of the eastern Great Lakes region of southern Ontario. 24th Int. Geol. Congr. Montreal, Que. Guide Book A 42: 75 p.

Dreimanis, A., and J. Terasmae. 1958. Stratigraphy of Wisconsin glacial deposits of Toronto area, Ontario. Geol. Assoc. Can. Proc. 10: 119–136.

Duane, D. B. 1967. Characteristics of the sediment load in the St. Clair River, p. 115–132. *In* Proc. 10th Conf. Great Lakes Res. Int. Assoc. Great Lakes Res.

Dussart, B. 1948. Recherches hydrographiques sur le lac Leman. Ann. Stn. Cent. Hydrobiol. Appl. 2: 187–206.

Edgington, D. N., and E. Callender. 1970. Minor element geochemistry of Lake Michigan ferromanganese nodules. Earth Planet. Sci. Lett. 8: 97–100.

Farrand, W. R. 1969. The Quaternary history of Lake Superior, p. 181–197. *In* Proc. 12th Conf. Great Lakes Res. Int. Assoc. Great Lakes Res.

Forel, F. A. 1895. Le Leman: monographic limnologique, Vol. 2. Mecanique, chimie, termique, optique, acoustique. F. Rouge, Lausanne.

Freeman, N. G., T. S. Murty, and W. S. Haras. 1972. A study of a storm surge on Lake Huron, p. 21. *In* Coll. Abstr. 3rd Can. Oceanogr. Symp.

Fricbergs, K. S. 1970. Erosion control in the Toronto area, p. 751–755. *In* Proc. 13th Conf. Great Lakes Res. Int. Assoc. Great Lakes Res.

Gadd, N. R. 1971. Pleistocene geology of the central St. Lawrence lowland. Geol. Surv. Can. Mem. 359: 153 p.

Gould, H. R., and T. F. Budinger. 1958. Control of sedimentation and bottom configuration by convection currents, Lake Washington, Washington. J. Mar. Res. 17: 183–198.

Great Lakes Levels Board. 1968. Publication on shoreline physical characteristics (by county). Can. Fed. Dep. Pub. Works, Ottawa.

Gross, D. L., J. A. Linebach, W. A. White, N. J. Ayer, C. Collinson, and H. V. Leland. 1970. Preliminary stratigraphy of unconsolidated sediments from the southwestern part of Lake Michigan. Ill. State Geol. Surv. Environ. Geol. Note 30: 20 p.

Gross, D. L., J. A. Linebach, N. F. Shimp, and W. A. White. 1972. Composition of Pleistocene sediments in southern Lake Michigan, USA. Sect. 8. Rep. 24th Int. Geol. Congr. Montreal, Que. 215–222.

Hands, E. B. 1970. A geomorphic map of Lake Michigan shoreline, p. 250–265. *In* Proc. 13th Conf. Great Lakes Res. Int. Assoc. Great Lakes Res.

Harriss, R. C., and A. G. Troup. 1969. Freshwater ferromanganese concretions, chemistry and internal structure. Science 166: 604–606.

Hartley, R. P. 1968. Bottom currents in Lake Erie, p. 398–405. *In* Proc. 11th Conf. Great Lakes Res. Int. Assoc. Great Lakes Res.

Hobson, G. D., and J. Terasmae. 1969. Pleistocene geology of the buried St. David's Gorge, Niagara Falls, Ontario: geophysical and palynological studies. Geol. Surv. Can. Pap. 68–67.

Hough, J. L. 1955. Lake Chippawa, a low stage of Lake Michigan indicated by bottom sediments. Bull. Geol. Soc. Am. 66.

Hough, J. L. 1958. Geology of the Great Lakes. Univ. Illinois Press, Urbana, Ill. 313 p.

1963. Geological and sedimentary characteristics of the freshwater environment. Univ. Mich. Great Lakes Res. Div. Publ. No. 10: 134–139.

Jensen, S., and A. Jernalov. 1969. Biological methylation of mercury in aquatic organisms. Nature. 223: 753–754.

Karrow, P. F. 1967. Pleistocene geology of the Scarborough area. Ont. Dep. Mines, Geol. Rep. 46: 108 p.

1969. Stratigraphic studies in the Toronto Pleistocene. Geol. Assoc. Can. Proc. 20: 4–16.

Karrow, P. F., J. R. Clark, and J. Terasmae. 1961. The age of Lake Iroquois and Lake Ontario. J. Geol. 69: 659–667.

Kemp, A. L. W. 1969. Organic matter in the sediments of Lake Ontario and Erie, p. 237–249. *In* Proc. 12th Conf. Great Lakes Res.

1971. Organic carbon and nitrogen in the surface sediments of Lakes Ontario, Erie and Huron. J. Sediment. Petrol. 41: 537–548.

Kemp, A. L. W., T. W. Anderson, R. L. Thomas, and A. Mudrochova. 1973. Sedimentation rates and recent sediment history of lakes Ontario, Erie and Huron. J. Sediment. Petrol. (In press)

Kemp, A. L. W., C. B. J. Gray, and A. Mudrochova. 1972. Changes in C, N, P and S in the last 140 years in three cores from lakes Ontario, Erie and Huron, p. 251–279. *In* H. E. Allen and J. R. Kramer [ed.] Nutrients in natural waters. John Wiley and Sons, New York, N.Y.

Kemp, A. L. W., and C. F. M. Lewis. 1968. A preliminary investigation of chlorophyll degradation products in the sediments of lakes Erie and Ontario, p. 208–229. *In* Proc. 11th Conf. Great Lakes Res. Int. Assoc. Great Lakes Res.

Kennedy, E. J., R. R. Ruch, and N. F. Shimp. 1971. Distribution of mercury in unconsolidated sediments from southern Lake Michigan. Ill. State Geol. Surv. Environ. Geol. Note No. 44.

Kindle, E. M. 1932. Lacustrine concretions of manganese. Am. J. Sci. 24: 496–504.

Kirk, J. F. 1962. An analysis of the bottom sediments of Lake Erie. M.A. Thesis. Univ. Toronto, Toronto, Ont. 177 p.

Kleerekoper, H. 1961. The significance of trace elements in freshwater plankton for the identification of microstratification in lake bottom sediments, with special reference to strontium. Univ. Mich. Great Lakes Res. Div. Publ. 7: p. 64.

Kovacik, T. L., and L. J. Walters. 1973. Mercury distribution in sediment cores from western Lake Erie. *In* Proc. 16th Conf. Great Lakes Res. Int. Assoc. Great Lakes Res. (In press)

Krauskopf, K. B. 1957. Separation of manganese from iron in sedimentary processes. Geochim. Cosmochim. Acta. 12: 61–84.

Lee, A. H. 1972. Some thermal and chemical characteristics of Lake Ontario in relation to space and time. Inst. Environ. Sci. Eng. Great Lakes Inst. Div. Rep. EG-6. Univ. Toronto, Toronto, Ont.

Lewis, C. F. M. 1969a. Quaternary geology of the Great Lakes p. 63–64. *In* R. G. Blackadar [ed.] Report on activities, Part A, April to October 1968. Surv. Can. Pap. No. 69–1A.

1969b. Lake Quaternary history of lake levels in the Huron and Erie basins, p. 250–270. *In* Proc. 12th Conf. Great Lakes Res. Int. Assoc. Great Lakes Res.

Lewis, C. F. M., and R. M. McNeely. 1967. Survey of Lake Ontario bottom deposits, p. 133–142. *In* Proc. 10th Conf. Great Lakes Res. Int. Assoc. Great Lakes Res.

Lewis, C. F. M., and P. G. Sly. 1971. Seismic profiling and geology of the Toronto waterfront area of Lake Ontario, p. 303–354. *In* Proc. 14th Conf. Great Lakes Res. Int. Assoc. Great Lakes Res.

Linebach, J. L., N. J. Ayer, and D. L. Gross. 1970. Stratigraphy of unconsolidated sediments in the southern part of Lake Michigan. Ill. State Geol. Surv. Environ. Geol. Note. No. 35.

McAndrews, J. H. 1972. Pollen analyses of the sediments of Lake Ontario. Sect. 8. 24th Int. Geol. Congr. Montreal, Que. 223–227.

McDonald, W. E. 1954. Variation in Great Lakes levels in relation to engineering problems, p. 249–257. *In* Proc. 4th Conf. Coastal Eng., Counc. Wave Res. Univ. Calif. Berkley, Calif.

Miller, R. L., and J. M. Zeigler. 1964. A study of sediment distribution in the zone of shoaling waves over complicated bottom topography, p. 133–153. *In* R. L. Miller [ed.] Papers in marine geology. Shepard Commemorative Volume.

Moore, J. R., R. P. Meyer, and R. Wold. 1972. Underwater exploration in Lake Superior prospects mapped in 1971. Offshore Tech. Conf. Pap. No. OTC 1648.

Mortimer, C. H. 1941. The exchange of dissolved substances between mud and water in lakes: J. Ecol. 29: 280–329.

Nussmann, D. G. 1965. Trace elements in the sediments of Lake Superior. Ph.D. Thesis. Univ. Michigan, Ann Arbor, Mich.

Pelletier, B. R. 1968. Submarine physiography, bottom sediments and models of sediment transport, p. 100–135. *In* P. J. Hood [ed.] Earth Sci Symp. on Hudson Bay.

1972. Clastic sediment ratios and environmental models. Coll. Abstr. 3rd Can. Oceanogr. Symp. Burlington, Ont. p. 37.

Perfil'ev, B. V., D. R. Gabe, A. M. Gal'perina, V. A. Rabinovich, Sapotnitskii, E. E. Sherman, and E. P. Troshanov. 1965. Applied capillary microscopy: The role of microorganisms in the formation of iron-manganese deposits. Consult. Bur. New York, N.Y. 122 p.

Potter, P. E., N. F. Shimp, and J. Witters. 1963. Trace elements in marine and freshwater argillaceous sediments. Geochim. Cosmochim. Acta. 27: 669–694.

Prest, V. K. 1970. Quaternary geology of Canada, p. 675–764. *In* R. J. W. Douglas [ed.] Econ. Geol. Rep. No. 1.

Price, N. B. 1967. Some geological observations on manganese-iron oxide nodules from different depth environments. Mar. Geol. 5: 511–538.

Robertson, A., and C. F. Powers. 1968. Comparison of the distribution of organic matter in the five Great Lakes: studies on the environment and eutrophication of Lake Michigan. Univ. Mich. Great Lakes Res. Div. Spec. Rep. No. 30: 258 p.

Rodgers, G. K. 1968. Heat advection within Lake Ontario in spring and surface water transparency associated with the thermal bar, p. 480–486. *In* Proc. 11th Conf. Great Lakes Res. Int. Assoc. Great Lakes Res.

Rossmann, R., and E. Callender. 1968. Manganese nodules in Lake Michigan. Science. 162: 1123–1124.

1969. Geochemistry of Lake Michigan manganese nodules, p. 306–316. *In* Proc. 12th Conf. Great Lakes Res. Int. Assoc. Great Lakes Res.

Rukavina, N. A. 1969. Nearshore sediment survey of western Lake Ontario, methods and preliminary results, p. 317–324. *In* Proc. 12th Conf. Great Lakes Res. Int. Assoc. Great Lakes Res.

1970. Lake Ontario nearshore sediments, Whitby to Wellington, Ontario, p. 266–273. *In* Proc. 13th Conf. Great Lakes Res. Int. Assoc. Great Lakes Res.

Saylor, J. H. 1966. Modification of nearshore currents by coastal structures. Lake Surv. Dist. Corps Eng., Detroit, Mich. misc. paper.

Schoettle, M., and G. M. Friedman. 1971. Freshwater iron-manganese nodules in Lake George, New York. Geol. Soc. Am. Bull. 82.

Scott, J. T., P. Jekel, and M. W. Fenlon. 1971. Transport in the baroclinic coastal current near the south shore of Lake Ontario in early summer, p. 640–653. *In* Proc. 14th Conf. Great Lakes Res. Int. Assoc. Great Lakes Res.

Seibold, E. 1967. La Mer Baltique prise comme modèle de géologie marine. Rev. Géogr. Phys. Géol. Dyn. (2), Vol. IX, Fasc. 5: 371–384.

SEIBOLD, E., N. EXON, M. HARTMANN, F. C. KOGLER, H. KRUMM, G. F. LUTZE, R. S. NEWTON, AND F. WERNER. 1971. Marine geology of Kiel Bay, p. 209–235. *In* Sedimentology of parts of central Europe guide book VIII. Int. Sediment. Congr. 1971.

SHIMP, N. F., H. V. LELAND, AND A. W. WHITE. 1970. Distribution of major, minor, and trace constituents in unconsolidated sediments from southern Lake Michigan. Ill. State Geol. Surv. Environ. Geol. Note 32: 19 p.

SHIMP, N. F., J. A. SCHLEICHER, R. R. RUCH, D. B. HECK, AND H. V. LELAND. 1971. Trace element and organic carbon accumulation in the most recent sediments of southern Lake Michigan. Ill. State Geol. Surv. Environ. Geol. Note 41: 25 p.

SIMONS, T. J., AND D. E. JORDAN. 1972. Computed water circulation of Lake Ontario for observed winds 20 April–14 May 1971. Can. Cent. Inland Waters Pap. No. 9.

SLY, P. G. 1966. Marine geological studies in the eastern Irish Sea and adjacent estuaries, with special reference to sedimentation in Liverpool Bay and the River Mersey. Ph.D. Thesis. Univ. Liverpool.

1973. The significance of sediment deposits in large lakes and their energy relationships, p. 383–396. *In* Proc. Symp. Hydrology of lakes (I.A.H.S.–A.I.S.H. pub 109), Helsinki.

SLY, P. G., AND C. F. M. LEWIS. 1972. The Great Lakes of Canada — Quaternary geology and limnology. 24th Int. Geol. Congr. Montreal, Que. Guide Book Trip A 43: 92 p.

SMITH, P. A., AND J. R. MOORE. 1972. The distribution of trace metals in the surficial sediments surrounding Keweenaw Point, upper Michigan, p. 383–393. *In* Proc. 15th Conf. Great Lakes Res. Int. Assoc. Great Lakes Res.

ST. JOHN, B. E., P. G. SLY, AND R. L. THOMAS. 1972. The importance of sediment studies in western lakes as a key to basin management, p. 145–174. *In* Proc. Symp. on lakes of Western Canada, Univ. Alberta, Edmonton, Alta.

SWAIN, F. M., AND PROKOPOVICH. 1957. Stratigraphy of upper part of sediments of Silver Bay area, Lake Superior. Geol. Soc. Am. Bull. 68: 527–542.

THOMAS, R. L. 1969a. A note on the relationship of grain size, clay content, quartz and organic carbon in some Lake Erie and Lake Ontario sediments. J. Sediment. Petrol. 39: 803–809.

1969b. The qualitative distribution of feldspars in surficial bottom sediments from Lake Ontario, 364–379. *In* Proc. 12th Conf. Great Lakes Res Int. Assoc. Great Lakes Res.

1972. The distribution of mercury in the sediments of Lake Ontario. Can. J. Earth Sci. 9: 636–651.

1973. The distribution of mercury in the surficial sediments of Lake Huron. Can. J. Earth Sci. 10: 194–204.

THOMAS, R. L., A. L. W. KEMP, AND C. F. M. LEWIS. 1972. Distribution composition and characteristics of the surficial sediments of Lake Ontario. J. Sediment. Petrol. 42: 66–84.

1973. The surficial sediments of Lake Huron. Can. J. Earth Sci. 10: 226–27.

TROSTELL, L. J., AND D. J. WYNNE. 1940. Determination of quartz (free silica) in refractory clays. J. Am. Ceram. Soc. 23: 18–22.

VERNET, J. P., AND R. L. THOMAS. 1972. The occurrence and distribution of mercury in the sediments of the Petit Lac (Western Lake Geneva) Eclogae Geol. Helv. 65: 307–316.

WILLIAMS, J. D. H., AND T. MAYER. 1972. Effects of sediment diagenesis and regeneration with special reference to lakes Erie and Ontario, p. 281–315. *In* H. E. Allen and J. R. Kramer [ed.] Nutrients in natural waters. Wiley and Sons, New York, N.Y.

WILLIAMS, J. D. H., J. K. SYERS, S. S. SHUKLA, AND R. L. HARRIS. 1971. Levels of inorganic and total phosphorus in lake sediments as related to other sediment parameters. Environ. Sci. Technol. 5: 113–1120.

WOOD, J. M., F. S. KENNEDY, AND C. G. ROSEN. 1968. Synthesis of methylmercury compounds by extracts of a methanogenic bacterium. Nature 220: 173–174.

WOODROW, R. L., R. G. SUTTON, AND N. A. RUKAVINA. 1967. A drowned beach in Lake Ontario west of Rochester, New York, p. 157–161. *In* Proc. 10th Conf. Great Lakes Res. Int. Assoc. Grea Lakes Res.

Changes in the Fish Species Composition of the Great Lakes[1,2]

W. J. CHRISTIE[3]

Fish and Wildlife Research Branch
Ontario Ministry of Natural Resources, Maple, Ont.

CHRISTIE, W. J. 1974. Changes in the fish species composition of the Great Lakes. J. Fish. Res. Board Can. 31: 827–854.

This paper is an interpretive review of the "case histories" which documented the changes in each of the Laurentian Great Lakes for the 1971 symposium on Salmonid Communities in Oligotrophic Lakes (SCOL). It suggests that lakes Huron, Michigan, and Superior passed through a parallel series of stock changes after the invasions of those lakes by the sea lamprey. First, the lake trout and burbot stocks collapsed, and then with the relaxation of predation pressure rainbow smelt, deepwater cisco, and alewife stocks increased. Lake herring stocks collapsed in apparent response to the smelt increase. Whitefish were affected by sea lamprey but recovery after the control of the lamprey in lakes Michigan and Superior suggested that the exotic species had little influence. Lake Ontario differed from the other lakes in that it was inhabited by both sea lamprey and alewife before the turn of the century, and provided the reservoir from which these species expanded to colonize the upper lakes. Alewife apparently equilibrated early, but the evidence was that more recent perturbations allowed the sea lamprey to become a significant factor in the loss of the piscivores of Lake Ontario. Subsequent proliferation of ciscoes and smelt, and collapse of the herring, followed a sequence similar to that of the upper lakes. Lake Erie seemed to be similarly affected by loss of predator stocks, but its predominantly eutrophic character made the situation more complex. Overfishing was indicted in many early stock collapses, in the early invasion of the smelt in lakes Huron and Michigan and in the recent cisco declines of lakes Ontario and Huron. Eutrophication and more direct pollution stresses had mainly inshore impacts, but the similarity in the species sequencing in the oligotrophic Great Lakes suggested that although these factors may have supplemented the other effects, their influence before about 1950 was less than that of overfishing and the invasion of exotic species. Control of sea lamprey, overfishing, and eutrophication seemed attainable in the Great Lakes, but the only defense against further invasions by pest species appeared to be maintenance of sufficiently dense piscivore stocks to assure their suppression. Determining the levels of harvest appropriate to this provision will require intensified research.

CHRISTIE, W. J. 1974. Changes in the fish species composition of the Great Lakes. J. Fish. Res. Board Can. 31: 827–854.

Cet article est une revue interprétative des "dossiers" présentés lors du symposium de 1971 sur les communautés de Salmonoïdes des lacs oligotrophes (SCOL) pour illustrer les changements qui se sont produits dans chacun des Grands lacs laurentiens. On suggère que les lacs Huron, Michigan et Supérieur ont passé par une série parallèle de changements de stocks, après avoir été envahis par la lamproie marine. En premier lieu, les stocks de touladis et de lottes se sont affaissés, et ensuite, avec la diminution de la prédation, l'éperlan arc-en-ciel, le cisco de profondeur et le gaspareau ont augmenté. Les stocks de ciscos de lac se sont affaissés, apparemment en réponse à l'augmentation des populations d'éperlans. Le grand corégone a été affecté par la lamproie marine, mais le rétablissement qui s'est produit à la suite du contrôle de la lamproie dans les lacs Michigan et Supérieur suggère que les espèces exotiques ont eu peu d'influence. Le lac Ontario diffère des autres

---

[1] This paper, part of a special issue that comprises a comprehensive review of Limnology in Canada, was prepared to mark the 19th Congress of the International Association of Limnology (SIL), in Winnipeg, Man., during August 1974.

[2] Contribution No. 74–4 of the Ontario Ministry of Natural Resources, Fish and Wildlife Research Branch, Maple, Ont.

[3] Present address: Glenora Fisheries Station, R.R. #4, Picton, Ont. K0K 2T0.

Printed in Canada (J3300)

lacs en ceci qu'il contenait à la fois la lamproie marine et le gaspareau avant le début du siècle, et qu'il a servi de réservoir à partir duquel ces espèces se sont répandues pour coloniser les lacs situés en amont. Le gaspareau semble s'être stabilisé tôt, mais on a des preuves que des dérangements récents ont permis à la lamproie marine de devenir un facteur important dans la perte des piscivores du lac Ontario. La prolifération subséquente des ciscos et de l'éperlan, ainsi que l'affaissement du cisco de lac ont suivi une marche semblable à celle des autres lacs. Le lac Erié a semblé affecté de la même façon par la perte de stocks de prédateurs, mais son caractère essentiellement eutrophe a compliqué la situation. Il y a preuve de pêche à outrance dans l'affaissement de bien des stocks au début, dans l'invasion précoce de l'éperlan dans les lacs Huron et Michigan, et dans le déclin récent des ciscos des lacs Ontario et Huron. L'eutrophisation et les contraintes plus directes dues à la pollution ont eu un impact surtout près des rives, mais la ressemblance dans la succession des espèces dans les Grands lacs eutrophes suggèrent que, bien que ces facteurs puissent avoir apporté leur contribution, leur influence avant 1950 environ a été moins forte que la pêche à outrance et l'invasion d'espèces exotiques. Le contrôle de la lamproie marine, la pêche à outrance et l'eutrophisation ont semblé réalisables dans les Grands lacs, mais la seule défense contre d'autres invasions d'espèces indésirables semble résider dans le maintien de stocks de piscivores suffisamment abondants pour assurer la suppression des pestes. On devra intensifier la recherche en vue de déterminer les niveaux de récolte appropriés.

Accepted January 31, 1974

MUCH has been written in recent years concerning the swift and extreme depreciation of the fish stocks of the Laurentian Great Lakes. The richest source of material to be found on the subject is the proceedings of a symposium concerned with salmonid communities in oligotrophic lakes (SCOL), held in Ontario in 1971. Its purpose was to isolate the relative impacts of man's chief effects on the fish by means of comparing and contrasting the fish stock histories of 19 large, north temperate zone lakes. Case histories were prepared for each of the Laurentian Great Lakes (Berst and Spangler 1972, 1973; Christie 1972, 1973; Hartman 1972, 1973; Lawrie and Rahrer 1972, 1973; Wells and McLain 1972, 1973), and each provided an interpretive review of relevant literature. To draw these works together, summary papers were prepared to find parallels among the effects of cultural eutrophication (Colby et al. 1972), of overexploitation (Regier and Loftus 1972), and the effects of new species introductions (Christie et al. 1972), as they occurred in the various lakes.

The present work is a summary review of the Great Lakes case histories and related studies, such as the exhaustive works of Smith (1964, 1968, 1970, 1972a, 1972b), and updates the data series on which these papers were based in order to confirm or refute the interpretations of trends by the SCOL authors. In most cases, I have relied strictly on the inferences drawn by the authors, and it is hoped that where my conclusions have differed from theirs, I have adequately presented their views. It is an obvious failing that the data available for interpretation of changes in fish stocks permit various perspectives to produce differing results, or that a few additional data points can produce significant changes. Intensive remedial measures for the Great Lakes fisheries are underway, or imminent, and it is vital that the most current data and all points of view be available to decision-makers. This paper is offered in response to these needs.

The earliest studies of Great Lakes fishes were undertaken by ichthyologists. Their works contributed not only to the taxonomy, but also to the life history and contemporary status of many taxa. In the past 40 yr, there have been many studies of particular species populations as well. These were directed mainly at economically important commercial or game fish stocks which were in difficulty, and these studies were also important as background for the lake case histories. The critical statistics on which all long-term studies have depended, however, are the reports of the commercial fisheries (Baldwin and Saalfeld 1962 with 1970 addenda). In the earliest days the records were incomplete and sporadic, but they do provide a chronicle of the changes in the fisheries for every jurisdiction in the Great Lakes dating from the 1860s. As they concern only those species which were marketed in any era, many species were not included. This is an important omission, but fisheries biologists generally believe that the commercially important species constituted most of the fish biomass in the various lakes. A more important criticism is that, until quite recently, commercial fishermen were not required to report fishing effort appliedto the fish stocks; consequently, in the main, inferences concerning long-term changes must be drawn from catch, rather than relative abundance estimates.

The following is an outline of recent patterns of fish stock change which have been common to the Great Lakes. Even the identification of coincident events remains equivocal, mainly because of the last-mentioned difficulty. The catch of stock b may change in response to a change in stock a, simply because the change in stock a made b either more or less attractive to the commercial fishery. Determining causality is even more difficult as the conventional methods of fishery science have not permitted measurement of the effect of any one of the major stresses on a fish stock, much less discernment of the component impacts when more than one stress is at work — and this is the case in all of the Great Lakes. To an extent this reflects the fact that there are few biological data series of sufficient length, sophistication, or breadth to yield estimates of the variations in natural and fishing mortality rates. These imposing problems led to the "compare and contrast" approach used in the SCOL symposium. This approach is also used in this paper but it must be stressed that defining coincidences leads to tentative inferences only, and at best yields only hypotheses for future testing.

Physical and Chemical Characteristics of the Great Lakes

As this subject has been dealt with at length elsewhere, only a brief orientation is offered here. Table 1 has been modified from Ryder (1972) and gives the pertinent statistics.

Of particular interest in these data are the marked north-to-south differences in summer temperature, and the trend from low mineralization and

TABLE 1. Climatic, watershed, physical, and chemical features of the Great Lakes (from Ryder 1972).

Item	Lake Superior	Lake Michigan	Lake Huron	Lake Erie	Lake Ontario
			Climatic		
Forest region[a]	GL–SL, Boreal	GL–SL Deciduous	GL–SL Deciduous	Deciduous	GL–SL Deciduous
Climatic region[b]	Dfb	Dfb	Dfb, Dfa	Dfb, Dfa	Dfb
Mean July temp (*C*)	16–18	18–21	18–24	21–24	21–24
Precipitation (*cm*)	60–100	60–100	60–100	60–100	60–100
Growing season (days)	140–160	160–200	160–240	220–240	200–220
			Morphometric		
Lake area (km^2)	82,414	58,016	59,596	25,719	19,477
Depth (*m*)					
maximum	397	285	229	64	237
mean	148	84	60	18	80
Shoreline length (*km*)	3,000	2,210	2,700	1,200	1,380
Shoreline development	2.9	2.6	3.1	2.1	2.8
Drainage area (km^2)	227,376	117,741	128,490	58,530	70,655
Altitude (*m*)	184	177	177	174	75
			Chemical		
TDS[c]	60	118	108	133	134
TA[d]	46	113	82	95	93
pH	7.9	8.2	8.1	8.1	8.0
Secchi disc (*m*)	10.0	6.0	9.5	4.5	5.5
Turbidity (JTU)	0.4	1.2	0.6	1.4	1.2

[a] GL–SL — Great Lakes–St. Lawrence Forest Region (after Rowe 1959).

[b] Dfb — cool summer but no dry season (northern Lake Michigan, eastern Lake Erie); Dfa — warm summer but no dry season (southern Lake Michigan, western Lake Erie).

[c] Total dissolved solids. Earliest available data.

[d] Total alkalinity. Earliest available data.

clean water in Lake Superior to heavier mineral loading and more turbid waters in the lower lakes. Ryders' (1972) data were selected, as indicated in the table, to represent the earliest available chemical data, but they obviously do not represent presettlement conditions. It is a reasonable inference, however, that drainage from the Laurentian Shield of the north always produced less fertile water than drainage through the sedimentary rock and glacial tills of the south. The effect is also accumulative, of course, with Lake Ontario water containing higher concentrations from the whole drainage.

Beeton (1965) compiled the available water chemistry data series for the lakes, and showed that whereas Lake Superior has remained effectively unchanged since the first analyses in the last century, the other lakes began to change at the turn of the century. The rate of increase in the levels of most of the major ions and in total dissolved solids was intermediate for lakes Huron and Michigan, and high for lakes Erie and Ontario. That mineralization of the water increased at about the same rate in lakes Erie and Ontario reflects the fact that some 85% of the water for Lake Ontario comes from Lake Erie. Lake Huron water, by contrast, is less rich than that of Lake Michigan because of the dilution effect of the Lake Superior outflow. Although increases in calcium, sodium plus potassium, chlorides, and sulphates have been pronounced in lakes Erie and Ontario, only chlorides and sulphates have increased significantly in lakes Huron and Michigan. This was interpreted as a major difference induced by pollution of the lower lakes (Beeton and Edmondson 1972).

The general correlate of the foregoing alterations in lake chemistry is the rate of human population growth. Figure 1 is redrawn from Beeton (1969) and illustrates this point. The chemical inputs represent the combined contributions of municipalities, industries, and the drainage from roads. Intensive agriculture of the more southerly parts of the drainage contributes further nutrient materials to the lakes, and also major silt burdens. Other aspects of the effects of human settlement will be discussed in later sections.

Fish Fauna

Hubbs and Lagler (1958) list 173 species of native and introduced fish, representing 94 genera and 29 families, in the Great Lakes and their tributaries. After the Pleistocene the lakes were recolonized from all three glacial refugia — Alaska, Mississippi, and Atlantic (Radforth 1944). Redis-

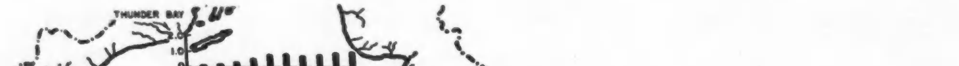

THUNDER BAY
2.0
1.0
0
1860 1880 1900 1920 1940 1960
LAKE SUPERIOR
DULUTH
SUPERIOR
ASHLAND
6.0
5.0
4.0
3.0
2.0
1.0
0
1840 1860 1880 1900 1920 1940 1960
MARQUETTE
LUDINGTON
FOND DU LAC
SHEBOYGAN
PORT WASHINGTON
MILWAUKEE
RACINE
KENOSHA
LAKE MICHIGAN
MUSKEGON
GRAND RAPIDS
HOLLAND
SOUTH HAVEN
BENTON HARBOUR
CHICAGO
JOLIET
HAMMOND
MICHIGAN CITY
2.0
1.0
0
1860 1880 1900 1920 1940 1960
GEORGIAN BAY
LAKE HURON
SAGINAW
BAY CITY
FLINT
PORT HURON
ST. CLAIRE
DETROIT
MONROE
TOLEDO
PT. PELEE
SANDUSKY
CHATHAM
LAKE ERIE
CLEVELAND
11.0
10.0
9.0
8.0
7.0
6.0
5.0
4.0
3.0
2.0
1.0
0
1820 1840 1860 1880 1900 1920 1940 1960
TORONTO
HAMILTON
WELLAND
NIAGARA FALLS
BUFFALO
KINGSTON
BELLEVILLE
PORT HOPE
WATERTOWN
LAKE ONTARIO
SYRACUSE
4.0
3.0
2.0
1.0
0
1800 1820 1840 1860 1880 1900 1920 1940 1960
0 25 50 75 100 mi

FIG. 1. Population trends in the various drainages of the Great Lakes (from Beeton 1969).

tribution produced rather similar mixes of fish in the five lakes. The open waters of the lakes became populated with two large piscivores, lake trout (*Salvelinus namaycush*)[4] and burbot (*Lota lota*). The subfamily Coregoninae was well represented and contributed a number of large planktivores and macrobenthos feeders. Lake whitefish (*Coregonus clupeaformis*) and shallow-water cisco (*Coregonus artedii*) were common to all lakes and both became important in the early commercial fishery. The two *Prosopium* species were localized varieties which never attained major biomass in the lakes. The deepwater ciscoes (or chubs) are a complex of highly plastic forms. Several subspecies have been identified, and recent shifts in taxonomic status, possibly owing to introgressive hybridization (Smith 1964), have been recognized, but the original array (considered a subgenus) basically consists of eight lesser coregonine species (including *C. artedii*). Of the deep-water forms, all seven were reported from lakes Michigan and Huron only (L. Wells personal communication), but the subgenus was well represented in all the lakes except Lake Erie, which has a more limited area of hypolimnion (Table 2).

The sculpins were another important group. There were four species whose distribution effectively covered the lakes. *Cottus bairdi* inhabits streams and protected shorelines. *C. cognatus* ranges mostly from the streams to approximately 90 m (Deason 1939) depth, and *Myoxocephalus quadricornis* has its major distribution below that. *Cottus ricei* ranges from the shore to about 140 m (Deason 1939).

Certain other species, like trout-perch (*Percopsis omiscomaycus*), several minnow species, darters, and sticklebacks, are also known to frequent the lakes down to intermediate depths; but of these, only emerald shiner (*Notropis atherinoides*) of Lake Michigan (Wells and McLain 1973) and spottail shiner (*Notropis hudsonius*) of Lake Erie (Regier et al. 1969) are known to have attained major biomass levels.

The nearshore waters contained a more diverse fish fauna, and here there are greater differences seen between lakes. First, areas like Saginaw Bay in Lake Huron, Green Bay in Lake Michigan, the Bay of Quinte in Lake Ontario, most of Lake Erie, and all of Lake St. Clair have extensive areas of shallow water which support profuse communities

TABLE 2. Representatives of the subfamily Coregoninae presently or formerly found in the Great Lakes.

Species	Lake				
	Superior	Michigan	Huron	Erie	Ontario
Coregonus nigripinnis blackfin cisco	×	×	×		×
Coregonus zenithicus shortjaw cisco	×	×	×		
Coregonus hoyi bloater	×	×	×		×
Coregonus reighardi shortnose cisco	×	×	×		×
Coregonus kiyi kiyi	×	×	×		×
Coregonus alpenae longjaw cisco		×	×	×	
Coregonus johannae deepwater cisco		×	×		
Coregonus artedii shallowwater cisco	×	×	×	×	×
Coregonus clupeaformis lake whitefish	×	×	×	×	×
Prosopium cylindraceum round whitefish	×	×	×		×
Prosopium coulteri pigmy whitefish	×				

---

[4] The names of fishes follow "A List of Common and Scientific Names of Fishes." Am. Fish. Soc. Spec. Publ. No. 6. 3rd ed. 1970.

of many varieties of the basically warmwater fishes. The steep basins of the main bodies of all lakes, except lakes Erie and St. Clair, have narrow littoral shelves and less abundant warmwater fish communities. There are, moreover, substantial climatic differences from north to south in the system, and many fishes from the Atlantic and Mississippi refugia were limited in their recolonization by the cold temperatures to the northward. Both the 18 C and 21 C July air temperature isotherms were identified by Radforth (1944) as important boundary lines. Table 3 is modified from Ryder (1972), and shows that the numbers of genera and species represented in each of the lower lakes are similar, but much reduced in lakes Huron and Superior. The differences between lakes Huron and Michigan are attributed to the broad climatic difference in Lake Michigan from extreme south to north. The 21 C July isotherm bisects Lake Ontario longitudinally, passes north of Lake Erie, south of both lakes Huron and Superior, and through Lake Michigan at about its north–south midpoint. The species excluded from Lake Superior include gars (Lepisosteidae), bowfin (Amiidae), freshwater drum (Sciaenidae), several catfishes (Ictaluridae), a number of minnows (Cyprinidae), and several sunfish species (Centrarchidae). The curvature of the isotherms from the southeast to the northwest, implied above, places the extreme western end of Lake Superior close to the 21 C July isotherm, whereas most of the Canadian waters eastward from approximately Thunder Bay, Ontario, have July temperatures averaging less than 18 C. This extensive area of Lake Superior is, on climatic grounds, apparently outside the range of many species like rock bass (*Ambloplites rupestris*) and smallmouth bass (*Micropterus dolomieui*), which are common elsewhere in the Great Lakes (Radforth 1944).

Lake Ontario occupied a special position in that it was colonized by at least three marine forms — Atlantic salmon (*Salmo salar*), threespine stickleback (*Gasterosteus aculeatus*), and perhaps sea lamprey (*Petromyzon marinus*), during the marine invasion (Champlain Sea – Gilbert Gulf stage

TABLE 3. Families of fishes native to the Great Lakes. Numbers denote numbers of genera and species found in each lake. Modified from Ryder (1972).

Family	Lake				
	Ontario	Erie	Michigan	Huron	Superior
Petromyzontidae	3–4	2–3	2–4	2–4	2–3
Acipenseridae	1–1	1–1	1–1	1–1	1–1
Lepisosteidae	1–1	1–2	1–2	1–2	–
Amiidae	1–1	1–1	1–1	1–1	–
Clupeidae	2–3	1–1	–	1–1	–
Salmonidae	4–10	2–4	4–13	4–12	4–12
Hiodontidae	1–1	1–1	–	–	–
Umbridae	1–1	1–1	1–1	1–1	1–1
Esocidae	1–4	1–3	1–3	1–3	1–2
Cyprinidae	11–33	12–33	11–31	8–24	8–20
Catostomidae	5–9	8–14	7–13	4–8	2–5
Ictaluridae	2–7	3–8	3–6	2–6	1–3
Anguillidae	1–1	1–1	–	–	–
Poeciliidae	1–1	1–2	1–3	1–1	–
Gadidae	1–1	1–1	1–1	1–1	1–1
Gasterosteidae	3–3	1–1	2–2	2–2	2–2
Percopsidae	1–1	1–1	1–1	1–1	1–1
Aphredoderidae	1–1	1–1	1–1	–	–
Percichthyidae	1–1	1–1	1–1	1–1	1–1
Centrarchidae	4–9	5–11	5–11	5–10	3–4
Percidae	5–12	5–17	4–13	5–14	4–7
Sciaenidae	1–1	1–1	1–1	1–1	–
Cottidae	2–4	2–4	2–4	2–4	2–4
Atherinidae	1–1	1–1	1–1	1–1	–
Families	25	24	21	21	15
Genera	56	55	52	46	34
Species	112	114	114	99	67

(Coleman 1922)). These and other species were apparently unable to take advantage of the Algonquin River (Coleman 1922) or earlier outlets to gain access to the upper lakes. Marine forms, including the introduced alewife (*Alosa pseudoharengus*), succeeded after a long passage of time in entering the upper lakes through the Welland Canal, which was opened in 1824 (Scott and Crossman 1973). The downward flow of fish from the upper lakes was sufficient to prevent many distinctive forms from developing in Lake Ontario. Some, possibly more sedentary fish like minnows and topminnows (Cyprinodontidae), have, however, developed distinctive east-west morphs, either because their progenitors persisted in different refugia, or because of segregation in postglacial times. The threespine stickleback may offer an example of replacement in Lake Ontario. In the upper Great Lakes the ninespine stickleback (*Pungitius pungitius*) is the only offshore form, but it was considered rare in Lake Ontario by Dymond et al. (1929) and has not been seen in recent years. The important blue pike (*Stizostedion vitreum glaucum*) and white bass (*Morone chrysops*) stocks of Lake Erie apparently maintained nonreproductive populations in Lake Ontario (Christie 1973) through escapement via Niagara Falls.

Interactions Between Fish Species

In lakes Superior, Michigan, Huron, and Ontario, the four Great Lakes which were historically oligotrophic, the principal fish stocks of offshore waters were the coregonines, lake trout, and burbot. Of these, only the burbot did not figure prominently in the commercial catch. Table 4 shows the high percentage of the total catch contributed by the coregonines and lake trout in the long term, and the drastic reduction which has occurred in recent years. The total fish catch has not declined so dramatically because the fisheries have shifted to other species in the absence of premium fishes. Replacements have been typically smaller fish like yellow perch (*Perca flavescens*), rainbow smelt (*Osmerus mordax*), or alewife. These species always have higher associated capture costs and lower market values than premium species. Bottom trawls and other technological developments have helped to ease overhead costs in some areas, but the general result of species composition changes has been a great reduction in gross revenue, and failure of many fishing enterprises.

The following discussion in this section deals with changes in the major species populations of concern in terms of possible effects of recently colonized "pest" fishes. Table 4 illustrates the fact that most of the major upheavals in all the Great Lakes except Lake Erie have happened in late years. For this reason I have been concerned mainly with the catch data for the years since 1940. Lake Erie represents a different and more complex situation, and is dealt with separately.

The first destabilizing events in this time frame are the establishment of lamprey populations in the various lakes. After the resulting collapses of predator stocks the four deep lakes were subjected to a number of further drastic stock changes. Smelt stocks swiftly increased in lakes Ontario and Superior. Alewife stocks burgeoned in the three upper lakes; cisco stocks increased, at least briefly, in all the lakes; and herring stocks collapsed. It is inferred in what follows that all these events had common causes.

THE SEA LAMPREY AND ITS IMPACT ON FISH STOCKS

The first generalized event (Fig. 2) in the collapse of the Great Lakes fisheries was loss of the lake trout. Coincident with these declines was the proliferation of the sea lamprey in each of the upper lakes.

The lamprey was known in Lake Ontario since the 1830s (Lark 1973) and it was thought most likely to be a marine relict present since the glacial retreat (Christie 1973). The creation of the Welland Canal theoretically gave it access to the upper lakes. That it did not successfully take advantage of this route at once is evidenced by the facts that the first official sightings were Lake Erie — 1921, Lake Huron — 1932, Lake Michigan — 1936, and Lake Superior — 1946. These dates, moreover, are well in advance of the first indications of proliferation in the various upper lakes. Interestingly, Bensley included the sea lamprey provisionally in his "Fishes of Georgian Bay" in 1915, on the basis of reports of sightings by commercial fishermen (Radforth 1944) of 15-inch lamprey on whitefish and trout. This account has been given little credence in recent years, but there are other examples of colonization which will be cited later, where the invaders were held to low numbers for extended time intervals after their initial penetration. One possible reason for the slow advance of the sea lamprey is that Lake Erie presents a serious ecological barrier. The lamprey never proliferated in that lake, for the likely reason that suitable habitat is limited (Hartman 1973). The cool water in Lake Erie during the summer is in the eastern basin and the warm waters of the central and western basins would seriously interfere with any upstream movement for a long period each year. Seasonal patterns in sea lamprey migratory movements have not, however, been studied.

TABLE 4. The contributions of the salmonid fishes to the yields of the oligotrophic Great Lakes. Species include lake trout, lake whitefish, deepwater ciscoes, and lake herring. Yields are in millions of kilograms averaged by 5-yr intervals.

	Lake Ontario			Lake Huron			Lake Michigan			Lake Superior			All Lakes		
	Catch of premium species	% of total	Total catch	Catch of premium species	% of total	Total catch	Catch of premium species	% of total	Total catch	Catch of premium species	% of total	Total catch	Catch of premium species	% of total	Total catch
1900–04	0.6	35	1.7	7.5	64	11.7	12.7	77	16.6	7.3	99	7.4	28.1	75	37.4
1905–09	1.0	56	1.8	7.0	64	10.9	17.8	83	21.5	5.4	95	5.7	31.2	78	39.8
1910–14	1.0	59	1.7	5.3	65	8.2	9.1	75	12.1	6.2	95	6.5	21.7	76	28.6
1915–19	1.7	65	2.6	6.7	68	9.9	9.5	77	12.4	6.9	93	7.4	24.9	77	32.3
1920–24	1.9	73	2.6	5.3	67	7.9	6.7	78	8.6	4.9	96	5.1	18.7	77	24.3
1925–29	1.5	71	2.1	6.6	73	9.0	7.9	79	10.0	8.3	97	8.6	24.2	82	29.7
1930–34	0.9	60	1.5	7.1	70	10.2	8.4	79	10.7	7.3	97	7.5	23.7	80	29.8
1935–39	1.1	61	1.8	6.3	69	9.2	7.3	66	11.0	9.0	98	9.2	23.7	76	31.2
1940–44	0.9	60	1.5	3.1	53	5.9	5.3	54	9.8	10.4	98	10.6	19.7	71	27.8
1945–49	0.4	36	1.1	2.2	48	4.6	8.1	73	11.1	9.4	98	9.6	20.1	76	26.4
1950–54	0.2	17	1.2	3.2	58	5.5	9.0	68	13.2	7.5	97	7.7	20.0	73	27.6
1955–59	0.2	18	1.1	1.2	38	3.2	6.2	50	12.4	7.2	96	7.5	14.8	61	24.2
1960–64	0.2	20	1.0	2.4	53	4.5	4.6	42	10.9	6.2	89	7.0	13.4	57	23.4
1965–68	.05	5	1.0	1.1	38	2.9	4.4	22	19.8	3.9	83	4.7	9.4	33	28.5

Regardless of the extent of, or reasons for, the delay in the establishment of the lamprey in the upper lakes, the expansion of lamprey populations in the various lakes was coincident with collapse of the resident trout fisheries, and the collapses occurred in the order of first appearance of the lamprey (Moffett 1958) (see Fig. 3). Moreover, Fry (1953) showed quite conclusively that the lamprey effectively exterminated the lake trout population of South Bay, Lake Huron.

The earliest attempts to control the sea lamprey were made by means of mechanical and electrical barriers in streams (Baldwin 1968). Even though these barriers were not altogether successful, and were later replaced by other control methods, barriers have been used in a few rivers until the present to monitor the relative size of the lamprey spawning run each year. The data in Fig. 3 were obtained from these barriers (Lawrie 1970). The values represent total catches from a variable number of barriers in the early years, so they are not useful as relative abundance indices during the establishment periods. They do not differ in an important way from the more rigorously selected and corrected data of Smith (1968), however, and have the added advantage of illustrating the relative intensity of the early control program. From the peak years onwards the data are standardized. Lawrie (1970) found that the annual counts of lamprey at the various Lake Superior weirs in these later years were strongly correlated with each other. Furthermore, the frequency of wounds seen on sampled fish correlated with the weir counts. This suggests that the Lake Superior data at least were internally representative.

The apparently long association between lamprey and lake trout in Lake Ontario has been considerably discussed. Christie (1973) was of the view that the lamprey was an important fish mortality factor in Lake Ontario. Christie (1973) suggested that deforestation reduced lamprey spawning habitat by raising temperatures during the last century, and the creation of dams in the tributary streams further interfered with spawning. It was postulated, therefore, that sea lamprey populations recovered with the decline of agriculture and deterioration of dams in parts of the watershed during the present century, producing large numbers of lamprey during and after the peak of trout and whitefish

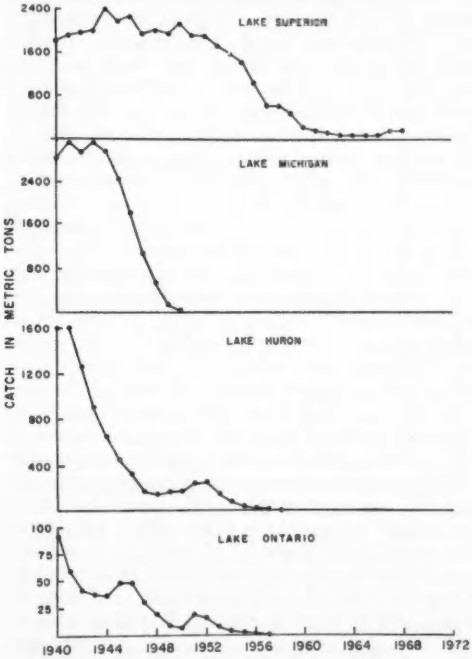


FIG. 2. Trends in the commercial yields of lake trout (*Salvelinus namaycush*) in the Great Lakes. Data from Baldwin and Saalfeld (1962) to 1968. Data from 1970–72 courtesy U.S. Bureau Sport Fisheries and Wildlife, Ann Arbor and Ontario Ministry of Natural Resources, Toronto.

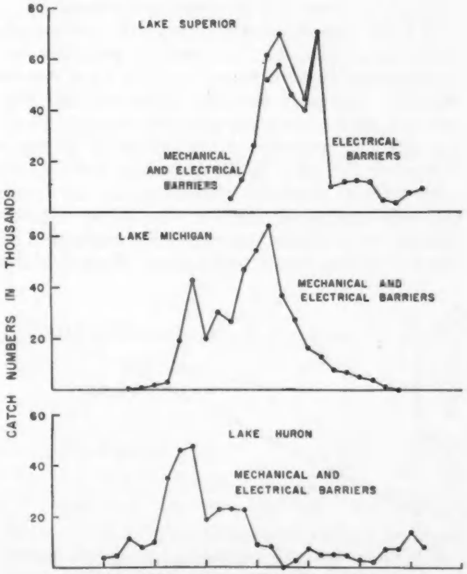


FIG. 3. Trends in the catches of sea lamprey (*Petromyzon marinus*) at control and monitoring barriers in the upper Great Lakes. Data from Lawrie (1970).

yields in the 1920s. Thereafter, it was suggested, less than fully favorable climate for reproduction, overfishing, and depredations of the lamprey population combined to cause collapse of the trout stocks and their extinction by 1950. Further, the impact of the lamprey was increased by its preference for the largest fish (Budd et al. 1969), which permitted it to function as a nonlethal parasite before man's intervention. As the fishery intensified, it reduced abundance of large, resistant fish, and the lamprey's effectiveness as a predator thus progressively increased.

Although the past events are speculative, the recent role of the sea lamprey in relation to both trout and whitefish mortality in Lake Ontario has some supporting evidence (Fig. 4). During the 1950s a series of experimental plantings of finclipped lake trout was made to assess mortality factors. As lamprey abundance levels fell during the decade, the survival of the trout improved. The trout were recaptured incidentally by the lake whitefish fishery. Relative abundance estimates based on catch-per-unit-effort statistics were used to calculate mortality at age 3 by means of Paloheimo's (1961) linear formula (Christie 1974). These estimates are compared in Fig. 4 with summer lamprey abundance estimates based on wound frequency in, and abundance of the whitefish stock (Christie 1974). The relation is linear and although it is described by only a few data points, the correlation is sufficiently strong to suggest that sea lamprey predation was an important factor in mortality of the trout. Annual mortality estimates for lake trout reached 70%, and virtually no trout ever survived to reach spawning age. The intercept of the line of fit in Fig. 4 represents the sum of instantaneous fishing, and other natural mortality coefficients. As the fishery regularly recaptured 25% of the initial numbers planted, most of this intercept value represents the effect of fishing, and it serves as an illustration that a deliberate gillnet fishery may be very effective in harvesting lake trout.

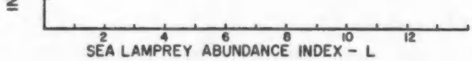


FIG. 4. Instantaneous lake trout mortality in relation to sea lamprey abundance in Lake Ontario during the 1950 decade.

The evidence in each of the lakes was that sea lamprey abundance remained high for some time after collapse of the trout stocks (Fig. 3), and that the lamprey utilized other, less preferred prey when the trout were gone. For example, in Lake Superior the yield of lake whitefish dropped from its 40-yr high of 0.9 million kg in 1952 to 182,000 kg in 1960 (Fig. 5). In lakes Michigan and Huron, the whitefish yield decline was similarly sharp and collapse was virtually complete by 1956 and 1968, respectively. In Lake Ontario there was evidence that lamprey pressure on whitefish was less rigorous in the 1940s when there were some trout and burbot remaining as prey, but that it increased in the early 1950s after whitefish became virtually the only prey. Thereafter, lamprey stocks declined and

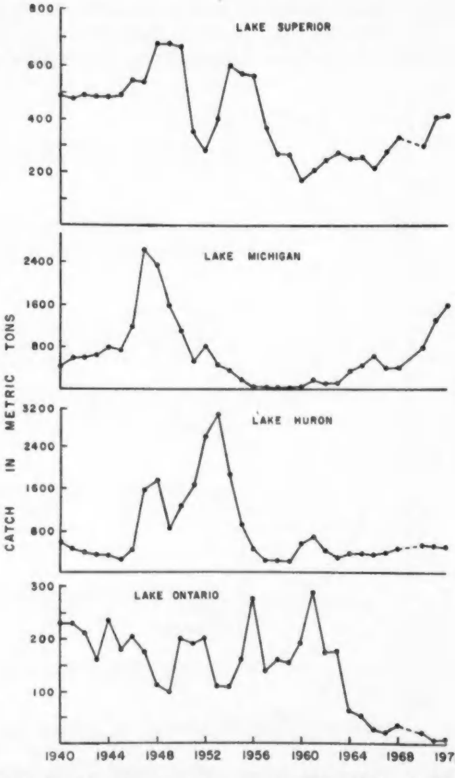


FIG. 5. Trends in the commercial yields of lake whitefish (*Coregonus clupeaformis*) in the Great Lakes. Data from 1970–72 courtesy U.S. Bureau Sport Fisheries and Wildlife, Ann Arbor and Ontario Ministry of Natural Resources, Toronto.

whitefish were not so heavily attacked (Christie unpublished data). Whitefish stocks collapsed in the early 1960s. By that time, shifts in biotic and abiotic conditions of both spawning and juvenile habitats had become apparent, as had the effects of excessive fishing and sea lamprey depredations. Thus no single cause for the decline could be isolated.

Other species fell prey to the lamprey as well as lake trout and whitefish. The burbot seems to have been a favored prey and stocks of the various lakes all collapsed along with lake trout (Smith 1968). As more favored prey became scarce, the lamprey utilized lake herring and larger individuals among the lesser coregonine species (Smith 1968). White suckers (*Catostomus commersoni*) were also preyed on and became scarce in each lake. To some extent excessive fishing was implicated in the collapse of all previously mentioned species, but suckers were the likely exception in that they have had little market appeal. It seemed unlikely, therefore, that declines in sucker yield could have resulted from shifts in fishing effort away from suckers at a time when preferred species were disappearing.

The effects of the sea lamprey both in Lake Ontario and the upper lakes were almost certainly more pervasive than the commercial fishery statistics have suggested. As numbers of their preferred prey species declined, the lamprey attacked many other species. The introduced rainbow trout (*Salmo gairdneri*), for example, were heavily attacked in all lakes (Berst and Wainio 1967), and this must have had extensive effects on stream biota. Round whitefish, although never abundant, are only rarely taken now in experimental nets along the north shore of Lake Ontario; however, some 15 yr ago they supported a small commercial fishery.

One positive effect of the sea lamprey was a resurgence of smaller species of the deep-water ciscoes in all four lakes after the predators were reduced in numbers (Fig. 6). This finding is scarcely surprising in light of the heavy dependence of both lake trout and burbot on ciscoes for food (Dymond 1928). These species were exploited more heavily after lake trout collapsed, and this resulted in higher yields. However, there are independent relative abundance indices in Lake Superior (Anderson and Smith 1971) and in Lake Michigan (Wells and McLain 1973), which indicate that real abundance increases occurred. It is inferred that the yield increase in Lake Huron also reflected an abundance increase.

Christie (1973) used indirect evidence to reach a similar conclusion about Lake Ontario ciscoes. After the decline of the piscivore stocks in the 1860s and again in the 1920s, the yield of ciscoes and herring increased sharply at the west end of the lake. This increase was accompanied by a significant increase in size of the fishing fleet during the 1930 decade, a situation likely to be associated with an increasing resource base.

The downward trends in the sea lamprey curves of Fig. 3 after the postinvasion maxima to some extent reflect the effects of control efforts. In 1955 the International Great Lakes Fishery Commission was formed, with the principal objective of finding means and coordinating efforts to limit sea lamprey populations and restore the trout. When it was clear that stream weirs were not sufficiently effective, the Commission sponsored a concerted search for selective toxicants. This search was rewarded with development of 3-trifluormethyl-4 nitrophenol (TFM) (Applegate et al. 1961). This compound has been used successfully since the early 1960s to eradicate the sedentary ammocoetes of the lamprey from the streams. The control program began in Lake Superior, and moved progressively through lakes Michigan and Huron and finally into Lake

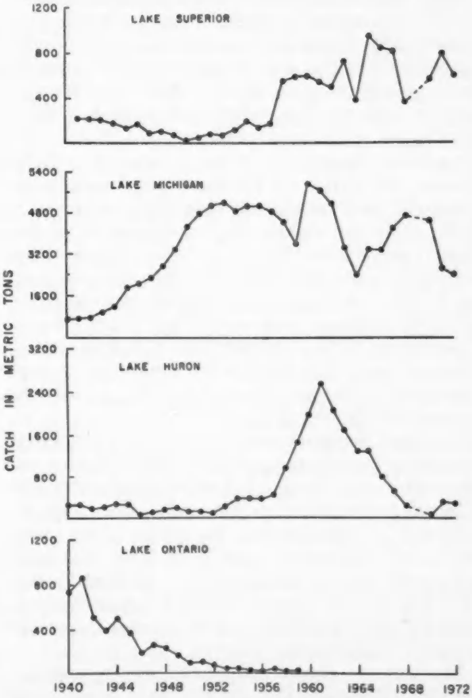


FIG. 6. Trends in the commercial yields of deepwater ciscoes (*Coregonus johannae*) in the Great Lakes. Lake herring (*Coregonus artedii*) and ciscoes are combined for Lake Ontario. Data from 1970–72 courtesy U.S. Bureau Sport Fisheries and Wildlife, Ann Arbor and Ontario Ministry of Natural Resources, Toronto.

Ontario in 1971. No control program was thought necessary in Lake Erie. The method seems to be effective in reducing the lamprey stocks to 10–15% of peak numbers (Lawrie 1970). Retreatment schedules designed to sustain such levels are prescribed at intervals determined by field surveys of ammocoete abundance.

The concommitant program to re-establish lake trout began in the late 1950s in Lake Superior. By the mid-1960s large hatchery brood stocks had been developed and were producing about 3 million trout for stocking, principally at 1 yr of age (Lawrie and Rahrer 1973). These fish increasingly dominated the inshore catches, until by the mid-1960s they contributed upwards of 95% of the trout taken in most areas of Lake Superior. The hatchery fish were, moreover, subject to progressively lower rates of mortality, as indicated by an approximately threefold increase in relative abundance between 1962 and 1969 (Lawrie and Rahrer 1973). Falling rates of lamprey wounding, correlated with the improving survival, permits the conclusion that lamprey control was proving effective. This recovery is not shown in Fig. 2 because the statistics in which it was observed were derived from experimental netting, whereas the commercial yield has been held to low levels by restrictions in both U.S. and Canadian waters. Although the numbers of sexually mature fish found on spawning shoals has been increasing also, naturally produced young fish have been slower in making their appearance in the catches, suggesting that natural reproduction may not yet be fully successful. The year 1973, in fact, marked the first time significant numbers of naturally produced fish have been seen (Great Lakes Fishery Commission 1973). Catches of lake whitefish in Lake Superior have been steadily improving for several years, and this is generally interpreted as a response to lamprey control (Fig. 4).

In Lake Michigan the early results of sea lamprey control are more impressive. Here, the rehabilitation program included extensive plantings of coho salmon (*Oncorhynchus kisutch*) smolts, and chinook salmon (*O. tschawytscha*) fingerlings, along with lake trout and several other salmonids. The lake trout and salmon stockings have resulted in the establishment of a highly successful sport fishery. Both whitefish and white sucker catches have also improved significantly (Fig. 5).

The lamprey control and rehabilitation programs for lakes Huron and Ontario have been undertaken more recently, and it is too early to judge their results. In the interests of these programs, the Province of Ontario (Tait 1970) has developed a strain of brook trout (*Salvelinus fontinalis*) × lake trout hybrids which have been selectively bred to combine the large size and deep-swimming habit of the lake trout with the early sexual maturity of the brook trout. The latter characteristic may provide more resistance to both the effects of fishing and the sea lamprey. The first plantings of F_4 and F_5 hybrids were made in Lake Huron in 1969. There have been indications of good survival and growth (G. R. Spangler personal communication), but it is not known at this date whether the fish have begun to reproduce.

Whereas there have been sharp reductions in sea lamprey runs to the barriers in each of the lakes following the initiation of the larvicidal treatments, it was only in Lake Superior that there was a truly dramatic collapse of the sea lamprey from its peak abundance levels. In lakes Michigan and Huron, slow declines had been in evidence for some years (Smith 1968). If the losses in trout yields seen in Fig. 2 even approximate the consumption of fish by the lamprey, the small numbers of lamprey taken at the weirs could scarcely have represented a significant fraction of the total lamprey population. Smith (1968) presented this illustration of the inefficiency of the early control measures in more detail.

Invasion of Smelt and its Effects

The rainbow smelt was introduced to the Great Lakes system in Crystal Lake, Michigan in 1912. First sightings in the Great Lakes were — Lake Michigan 1923; Lake Huron 1925; Lake Ontario 1929; Lake Superior 1930; and Lake Erie 1936 (Van Oosten 1937). The Lake Michigan and Lake Huron stocks built up quickly. In Lake Michigan a fishery had developed by 1931 and abundance increased sharply through the 1930s. The fishery developed later in Lake Huron, but evidently smelt proliferated at about the same time (Van Oosten 1937). By contrast, smelt populations of lakes Erie and Ontario did not become abundant until the late 1940s and the buildup in Lake Superior occurred gradually between 1952 and 1964 (Fig. 7).

The first sighting in Lake Erie was delayed somewhat, but appearances in the other lakes seem to relate to proximity to Crystal Lake. The time lags required before colonization, on the other hand, may have been in part due to delays in locating suitable habitat. In Lake Michigan, colonization was largely confined to Green Bay, and in Lake Huron to Saginaw Bay; both are large bays of shallow-to-moderate depth. The central basin of Lake Erie is comparable in morphometry to these bays, and the smelt population of that lake used the north shore of the central basin for spawning (MacCallum and Regier 1970). In Lake Superior, the largest expanse of shallow water is at the western end, which is the area of chief smelt concentration (Baldwin and

Saalfeld 1962). In Lake Ontario, smelt are much more broadly distributed and can be found in all parts at depths down to about 46 m.

A related, and perhaps stronger, explanation for the time lags is that the smelt had to overcome varying but generally high levels of environmental resistance in each lake. The sequence of colonization suggests this resistance may have been predation pressure. In both lakes Superior and Ontario, establishment occurred after the collapses of the piscivore stocks. The first buildups in lakes Huron and Michigan occurred during relatively minor reductions in trout catches (Baldwin and Saalfeld 1962). It may be of equal or greater significance that both Green Bay and Saginaw Bay, the two areas in which smelt especially proliferated, had low stocks of walleye (*Stizostedion vitreum vitreum*), and yellow perch during the 1920s (Hile 1937; El-Zarka 1959; Wells and McLain 1973). Therefore, the early delays possibly occurred while the smelt traversed the open lakes against strong predation pressure, and this pressure eased when they reached the bays. The first records of commercial and sporting catches in Lake Ontario were in the Bay of Quinte (Christie 1973), where walleye were scarce. It is presumed that Lake Superior stocks originated from Lake Huron or Lake Michigan, and that Lake Ontario stocks originated from Lake Erie (Christie 1973); if so, the fish had enormous distances to travel to the relatively protected areas, and prior to the piscivore declines, predation pressure would have been severe. In Lake Erie, Regier et al. (1969) suggested that hypolimnial oxygen depletion in the central basin in summer may have created a sanctuary for pelagic juveniles of smelt and perch, protecting them from predation by *Stizostedion* species, which use the bottom as the base from which they forage.

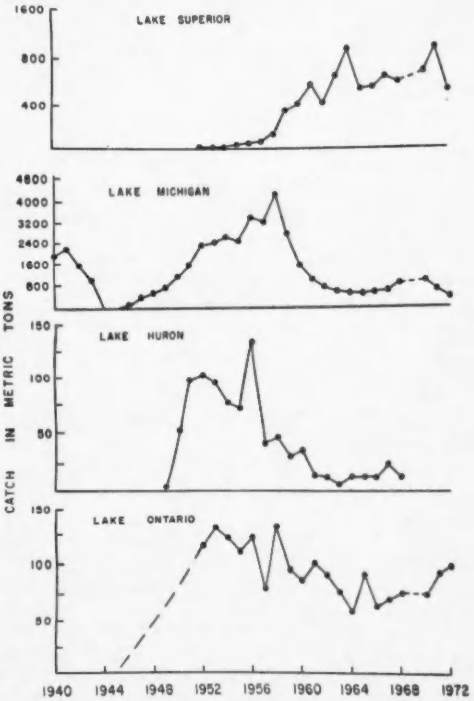


FIG. 7. Trends in the commercial yields of rainbow smelt (*Osmerus mordax*) in the Great Lakes. Data from 1970–72 courtesy U.S. Bureau Sport Fisheries and Wildlife, Ann Arbor and Ontario Ministry of Natural Resources, Toronto.

Smelt of lakes Michigan and Huron were subject to a drastic mortality during the winter of 1942–43 (Van Oosten 1947), and stocks were several years recovering from it. In Lake Michigan, yield levels built rather slowly from the extreme low of 1946 to a high in 1958. Allowing a 3-yr cycle (Baldwin 1948), 1948 was the earliest year the stocks could have reattained full abundance in Lake Huron. Recovery there coincided in a rough way with development of the fishery, and appears to have been complete by 1950.

Smelt have been suspected of many harmful effects on the native fish stocks of the Great Lakes. The sheer magnitude of numerical abundance makes it almost certain that their colonizations had at least locally significant impacts. The record yield in Lake Erie (1962) for example was 8.6 million kg, and that represented 30% of the entire catch of all species for that year. The smelt biomass was obviously a major component of the system. The diet of smelt, moreover, makes them suspect. The invertebrate diet of smaller smelt would place them in competition with many species, and the fish-eating habit of larger smelt would make them a serious predatory threat (Baldwin 1948) to less abundant species, even if annual fish consumption by each smelt was quite small.

One apparent reaction to smelt invasion which occurred with some consistency, was collapse of the lake herring stocks. In Lake Superior, collapse of the herring was swift and it occurred after smelt yields had risen to exceed about 454,000 kg/yr (Fig. 7 and 8). In Lake Michigan, herring yields declined during the first increase in smelt population, and then recovered briefly after the 1942–43 mortality (Fig. 8). In Lake Huron, lack of smelt catch statistics before 1948 limits the possibilities for interpretation. However, Lake Huron smelt also collapsed in 1943, and recovery of lake herring between 1944 and 1952 was possibly a result of collapse of the smelt. There are no separate statistics for lake herring for the whole of Lake Ontario, but it is known that smelt were scarce in the offshore waters, at least in 1942 (Stone 1947), and unlike the other lake situations this would imply the smelt increase occurred simultaneously with the herring collapse, rather than a few years in advance of it. A year-class produced as early as 1941, however, could have escaped detection by Stone's gillnets, and could have influenced survival of juvenile herring almost at once. There are no statistics with which to test this hypothesis, but it is known that a significant sport fishery for spawning smelt had developed by about 1945 (Christie 1973). As first-generation fish, these could not have been younger than 1943 year-class fish, and they could have easily been as old as members of a 1941 year-class. If a second or later generation was involved, it would be necessary to conclude that Stone's observations were not representative of the total smelt population in 1942, and that the increase in smelt population preceded collapse of the lake herring in Lake Ontario as well as the other lakes. In Lake Erie also, no more significant catches of herring were made after ascendency of the smelt, but catches of herring had continued so low from 1925 to 1946 that the significance of the final year-class (that of 1944), and the fate of its progeny, is unknown.

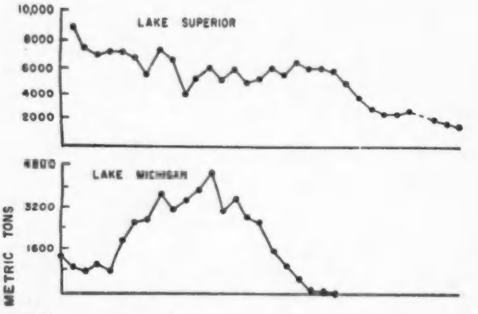


FIG. 8. Trends in the commercial yields of lake herring in the Great Lakes. Lake Ontario data are for the Bay of Quinte only. Data from 1970–72 courtesy U.S. Bureau Sport Fisheries and Wildlife, Ann Arbor and Ontario Ministry of Natural Resources, Toronto.

What makes the postulated relation between smelt and lake herring especially appealing is that both species have similar distributions and habits. Both are shore-spawning, thermocline-dwelling planktivores. Those areas like Green Bay, Saginaw Bay, and the western end of Lake Superior, to which smelt distribution is largely confined, were also the principal areas of herring production. Other factors influenced the herring stocks as well. In every lake except Lake Michigan there were serious declines in yield from levels in earlier periods, before smelt were a consideration at all. Large lake herring are also attacked by sea lamprey, and in some cases this must have been an additional stress. On the other hand, the fact that the herring of Lake Superior has not recovered yet as a result of reduction of the sea lamprey population (as was the case with the lake whitefish), argues against a major interaction between lamprey and lake herring.

Collapse of the smelt stocks coincided with production of a large 1943 year-class of whitefish in both Lake Huron and Lake Michigan (Wells and McLain 1973; Berst and Spangler 1973). Lake Superior whitefish increased in the face of a prospering smelt population, and Lake Ontario whitefish persisted long after the smelt invasion, however, which suggests that the two species do not interact significantly.

The next point of interest is that smelt catches have declined seriously in lakes Huron and Michigan, and slightly in Lake Ontario, since their post-invasion maxima. In Lake Superior smelt abundance has apparently levelled off (Anderson and Smith 1971). Smith (1970) argued that the explosive increases in populations of alewife were responsible for the effects in lakes Michigan and Huron, but this would not explain the decline in Lake Ontario.

INVASION OF THE ALEWIFE AND ITS EFFECTS

The origin of the alewife in the Great Lakes has not been established with certainty. Miller (1957) and earlier authors suggested that fry were inadvertently introduced to Lake Ontario in the early 1870s during an attempt to establish the American shad (*Alosa sapidissima*). Smith (1970), on the other hand, found that the species was in the Finger Lakes and the Erie Barge Canal system of New York State in the 1860s, and suggested that alewife may have reached Lake Ontario via the Mohawk and Hudson rivers. Smith (1970) also pointed out, however, that the species could have originated from stocks in the St. Lawrence River, and would have had access to Lake Ontario for thousands of years. Radforth (1944) considered it "not improbable" that the alewife was a relict of the marine invasion, and based this judgment mainly on the fact that alewife have been landlocked in some lakes in Frontenac and Leeds counties of Ontario since the recession of the Champlain Sea.

The exact origin does not seem as important as the fact that alewife could have penetrated from the St. Lawrence River and could have been present in the lake, but at abundance levels too low for detection by early ichthyologists. As in the case of smelt, establishment of the alewife is consistent with an hypothesis that the species only proliferates after relaxation of predation pressure (Miller 1957; Smith 1970).

The alewife only recently entered the commercial catch with development of a fishery in Lake Michigan (Wells and McLain 1973), so the statistical record is incomplete. Unlike other species, however, the alewife has made its presence known through periodic massive die-offs in the Great Lakes. Most authors have inferred that these mortalities became noticeable (Pritchard 1929) only after the alewife had achieved significant abundance. Graham (1956) suggested that the species had not fully adapted to the thermal structure of Lake Ontario. It was thought mortalities resulted when alewife ascended from their winter habitat in the depths of the lake towards their spawning areas, and traversed temperature gradients faster than they could acclimate. Heavy mortalities have been observed at irregular intervals since the 1890s in Lake Ontario. The most noteworthy mortalities after the invasion of the upper Great Lakes have been in Lake Michigan (Smith 1970). The implication has been that heavy (and readily observable) mortalities coincide with some combination of climatic conditions and population density, but the point has not been thoroughly investigated.

Penetration of the upper lakes by alewife was gradual. The first specimens in Lake Erie were reported in 1931 by Dymond (1932) — 58 yr after it was first observed in Lake Ontario. The first record in Lake Huron was in 1933 (MacKay 1934). Alewife were reported to occur in Lake Michigan in 1949 (Miller 1957), though not in Lake Superior until 1954.

The postinvasion effects of the planktivorous alewife on fish stocks of Lake Ontario are not understood. Smith (1970) suggested that the explosive increase of alewife, which was complete in Lake Ontario by the 1890s, caused collapses of lake herring and emerald shiner stocks immediately, and later caused declines in minor piscivore stocks, and perhaps even in whitefish. By contrast, Christie (1973) suggested that alewife acclimatized early, and even though they were likely subject to major stock oscillations from year to year, there was no evidence of trends in alewife stocks which could be related to subsequent stock changes. He further felt that although the emerald shiner and possibly other species may have been reduced in numbers by alewife, they cannot be implicated in the important recent changes in the fish stocks. A point on which both authors agree is that alewife proliferated in the lake during a period of low piscivore abundance. The Atlantic salmon (*Salmo salar*) had disappeared and both lake trout and burbot were relatively scarce in the 1890–1910 period (Christie 1963).

That Christie (1973) was unable to discern any recent increases in alewife abundance following disappearance of its major offshore predators and competitors, was especially curious. The only evidence is in the frequency or severity of alewife springtime mortalities, and it is not known how reliable this is as an index of alewife abundance. Index fishing since 1958 within the Bay of Quinte (Fig. 9) has revealed no trends in abundance, but the data do show annual oscillations in size of the spawning run, which vary tenfold; also some peaks are correlated with significant mortalities along the lakeshores. That some responses to the changes in offshore predator and competitor density levels have occurred is highly likely. That alewife stocks

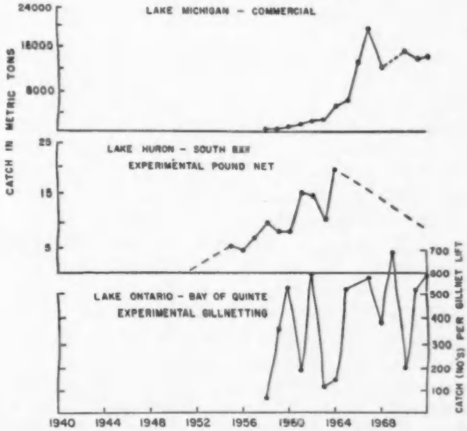


FIG. 9. Trends in the abundance of alewife (*Alosa pseudoharengus*) in the Great Lakes. Lake Michigan data are commercial yields from Baldwin and Saalfeld (1962), and courtesy U.S. Bureau Sport Fisheries and Wildlife, Ann Arbor and Ontario Ministry of Natural Resources, Toronto. Lake Huron data are from experimental poundnets in South Bay. Lake Ontario data are from experimental gillnets in the Bay of Quinte.

have evidently not undergone extreme changes like those seen in Lake Michigan may suggest that alewife stock density has been controlled in recent times to a more important extent by stocks of fish in nearshore areas, with which the alewife must associate for the first 1 or 2 yr of life.

Progression of the species into Lake Erie may have been impeded by the dense stocks of piscivores and potentially competitive planktivores living there. Smith (1970) noted that the first sighting coincided with a period of low yield of blue pike, walleye, and sauger (*Stizostedion canadense*). Alewife have never achieved high levels of abundance in Lake Erie, and Smith (1970) noted that the only years when die-offs were observed were 1952 and 1967, and these years were both in, or following, periods of predator decline.

Population increases in lakes Huron and Michigan were both delayed until after collapse of the lake trout (Fig. 2). The data in Fig. 9 are not strictly comparable, because the commercial fishery for alewife in Lake Michigan did not develop immediately. Wells and McLain (1973), however, describe the spread of the species from north to south in the lake after 1949, and the general increase to nuisance levels (for fishermen) by 1957. From that point the stocks continued an accelerated rate of increase until 1967, when the peak catch of 19 million kg was taken. After the maxima were reached, stocks of Lake Huron declined (Berst and Spangler 1973) and those of Lake Michigan have apparently stabilized (Fig. 9).

At least in a practical sense, invasion of the alewife was not as important in Lake Huron as it was in Lake Michigan. In the latter lake, the nuisance effects of alewife, whose mortalities caused windrows of dead fish along the shores and whose spawning runs at peak density clogged municipal and other water intakes, attracted wide public attention (Wells and McLain 1973). Berst and Spangler (1973) made no comment on the biological consequences of alewife colonization in Lake Huron. Alewife have not proliferated in Lake Superior, perhaps, as Scott and Crossman (1973) suggest, because the lake is too cold for the species.

Smith (1970), by contrast, associated the alewife explosion with declines in stocks of lake herring, deepwater ciscoes, smelt, and yellow perch in both lakes. Certainly, the biomass of alewife, as reflected in the huge commercial catches in Lake Michigan, had to be accommodated by other biota. Wells (1970) for example, showed striking changes in composition of the zooplankton associated with colonization of the lake by alewife.

Smith's (1970) postulated effects of the alewife raise some questions. First, as seen in the last section, collapses of lake herring stocks were more closely correlated with smelt stock increases. The suggested interaction with smelt and deepwater ciscoes cannot be reconciled with observations on Lake Ontario. There, smelt exploded in the presence of an abundant alewife stock (Graham 1956). The alewife, moreover, was apparently unable to capitalize on losses of the various cisco species during the 1930s, evidently losing out in competition with *Coregonus hoyi*. As pointed out above, any population increase of the magnitude of the alewife explosion in Lake Michigan was bound to affect many species, at least temporarily, but consistency requires the conclusion that neither smelt nor deepwater ciscoes are generally adversely affected by alewife. In the absence of any alternative answer, it is suggested that problems of the cisco stocks arose mainly from excessive fishing pressure. This does not of course imply that after the collapse of the cisco stocks, smelt and alewife populations did not contribute to their continued suppression. It is further proposed that the declines of alewife and smelt in Lake Huron and of smelt in Lake Michigan represent the returns of these stocks to equilibrium levels. If true, a decline of Lake Michigan alewife can be expected, but the burgeoning stocks of introduced salmonids in that lake may reduce the alewife stocks before the hypothesis can receive its test.

Effects of Overfishing

Just as eutrophication became obvious and worrisome during the 1950s, so commercial fishing effort also reached a climactic level of intensity. Starting around 1950, nylon began to replace cotton and linen as gillnetting material, and by about 1955, all gillnet fisheries of the lakes had been converted to it. This achieved at least a threefold increase in fishing intensity (McCombie and Fry 1960, Regier et al. 1969), with little compensating reduction in total fishing effort. The coincidence of this intensification with various shifts in the fish stocks after 1950 led to re-evaluation of the effects of fishing.

There are relatively few cases where fish stock collapses have been clearly identified as the result of overfishing. Loss of the lake sturgeon (*Acipenser fulvescens*) from all the lakes, by about the turn of the century, is generally accepted as one such case (Harkness and Dymond 1961). These fish require many years to achieve sexual maturity and evidently were also highly vulnerable to gillnets. There are other cases of elimination of localized spawning stocks of whitefish (Christie 1973) and lake herring (Lawrie and Rahrer 1973) through excessive fishing. Most documented cases occurred before major environmental changes, or before new fish species had arrived to complicate the interpretation.

During more recent times, even when collapse of a fish stock was documented fully by means of conventional biological statistics (cf. Parsons 1967), it has usually not been possible to produce a simple indictment of overexploitation. On the contrary, extreme stock fluctuations were found associated with great variability in year-class strength (cf. Hile 1937), and until quite recently fishery workers held that these were virtually entirely of natural origin. It was repeatedly demonstrated that extremely large year-classes could be produced from minimal brood stocks, and that these large year-classes often failed to beget large broods of progeny (Hile 1937; Scott 1951). A few studies associated year-class variability with climatic shifts. With smallmouth bass, for example, Fry and Watt (1957) found that warm summers were associated with large year-classes, and Christie (1963) found that early winters with early following springs were conducive to production of large whitefish year-classes in Lake Ontario. None of the earlier studies had sufficient data to define the real contribution of a large year-class in terms of replenishing the functional brood stock. The suspicion was growing by the late 1960s that intensive fishing affected the frequency with which large year-classes occurred, by maintaining brood stocks at levels which required near perfect environmental conditions for large year-class production (Christie 1968). Christie and Regier (1973) conducted the first Great Lakes analysis of this question on data from the eastern Lake Ontario whitefish fishery. Although the number of spawner year-classes whose history could be followed was limited, their data suggested that when the life expectancy of a year-class was reduced to the point where there was less than one opportunity on the average for a female fish to spawn, replacement of the year-class by its progeny did not occur, however favorable the weather. Further, it was found that longevity and the climatic variable were related such that shorter life span (i.e. lower lifetime spawn output per female) could be compensated by a greater frequency of favorable climatic conditions for reproduction, and conversely, greater longevity could compensate for a series of less than ideal spawning years. The concept that long-lived species compensate for environmental variations through a number of spawnings appears to be new to the Great Lakes area.

The consensus for many years was that fish stocks were protected by the economics of the fishing industry. That is, when catch-per-unit-effort in any fished stock dropped below a level where it was profitable to fish, the pressure eased and the stock recovered. Studies of later years have shown, however, that recovery does not always occur. Various authors (e.g. Christie 1968; Regier et al. 1969) have pointed out that if a fishery shifts its attention to a smaller species in the same area after collapse of a premium stock, and if this new fishery uses a smaller gillnet mesh size, the capture of juveniles of the premium species may in effect permanently suppress that species. More often, however, it has been observed that the premium stock can be reduced to the point where its normal ecological advantages are lost, and it is replaced by another species whether smaller mesh sizes are involved or not.

The best examples of fishery-induced stock replacement concern the deepwater ciscoes. The individual cisco species were not distinguished in the commercial fishery statistics, but periodic surveys revealed substantial changes in species composition. The blackfin cisco (*Coregonus nigripinnis*) and *C. johannae*, the two largest species, were the principal support for the early fisheries of Lake Michigan, but had become scarce by 1930–32 (Moffett 1957; Smith 1964). Four others — *C. zenithicus*, *C. alpenae*, *C. reighardi*, and *C. kiyi* — all of intermediate size, declined sharply between 1930–32 and 1960–61. The bloater (*C. hoyi*) on the other hand increased several-fold between 1930–32 and 1954–55, and this was the smallest and least valued of the ciscoes. The recent changes were at least in part caused by collapse of the lake trout and subsequent predation on larger coregonines by the sea lamprey, but loss of the first two species was almost indisputably the result of overexploitation.

Data were not sufficient to allow comparable analyses in lakes Superior or Huron, but early surveys of Lake Ontario revealed a similar sequence (Christie 1973). The largest cisco, *C. nigripinnis*, was thought to have become extinct around the turn of the century (Koelz 1926). *Coregonus kiyi* and *C. reighardi* were much reduced between 1927 (Pritchard 1931) and 1942 (Stone 1947), and the bloater proliferated and was virtually the only species left when collapse occurred in the mid-1940s. The sea lamprey was not thought involved in this sequence, because there were enough trout and burbot still remaining in the lake in the early 1940s to buffer the whitefish stocks, and it was felt that ciscoes should be even less preferred prey for lamprey than whitefish were. The only other factor which could be implicated, therefore, was overfishing.

In both lakes the fisheries progressed from large gillnet mesh sizes used for large ciscoes, through progressively smaller mesh sizes, as the species composition changed. It is possible that, as suggested above, the smaller mesh sizes cropped juveniles of the larger species and inhibited recovery after initial reduction. As noted earlier, however, cisco collapses of lakes Huron and Ontario and the evidently incipient collapse of Lake Michigan ciscoes did not likely represent fishing to depletion. Once sufficiently disadvantaged by fishing, it is suggested that the numerical superiority of prospering alewife and smelt stocks could readily account for the continued suppression, and even final demise of the ciscoes.

Lake trout yields of Lake Superior were quite steady for many years, but Hile et al. (1951) showed that yields were maintained through the 1930s and 1940s only through sharply increasing levels of fishing effort. No one has suggested that the sea lamprey was not the primary factor in the collapse of the trout stocks, but the implication that severely stressed stocks would be more vulnerable to lamprey cannot be taken lightly. Wells and McLain (1973) cited Van Oosten's (1949) description of the gradual decline in Lake Michigan trout yield between 1893 and 1938, which occurred in the face of greatly increasing fishing intensity, and raised the possibility that a less stressed stock might have better resisted the onslaught of the sea lamprey. In an earlier section I restated the hypothesis (Christie 1973) that the Lake Ontario lake trout could have been more resistant to lamprey before the onset of the fishery by reason of the greater numbers of large fish in the population.

In this connection, Lawrie and Rahrer (1973) laid considerable stress on the deficiency of catch and effort data available for use in attempting to detect overfishing. The zones used for summarization of the statistics are much larger than ranges of many individual component stocks. This was especially true of lake herring, which are typically fished on the spawning grounds, and highly localized. The fishery could sequentially decimate first local stocks and then stocks further from the home ports. The result in such circumstances (the sequence is in fact commonly observed in all of the Great Lakes and elsewhere in the world) (Regier and Loftus 1972) was that yield and effort could remain effectively constant in the statistics for many years before all stocks had been fished out and a general collapse was detectable.

It had become commonplace in the Great Lakes to view massive yield oscillations of many species as "normal." To the extent these variations were exaggerated by extreme reduction of the life span of the fish by fishing, however, this may well have been a danger sign which went unheeded. In walleye, blue pike, and whitefish it was shown (Parsons 1967, 1970; Christie and Regier 1973; Cucin and Regier 1966) that harvest levels could rise to the point where the fishery cropped each year-class thoroughly as it became large enough to enter the fishery. As pointed out above, the prospect now exists that these long-lived species must live for a certain minimum number of years to achieve stock replacement, and to retain their status in the system (Abrosov 1969).

Effects of Environmental Degradation

Examples of direct effects of habitat change on Great Lakes fish stocks have seldom been described. This is to a large extent because the effects of excessive fishing and appearance of the "pest" species have been more or less contemporary with major environmental changes. This is more obviously true in the lower Great Lakes than in the upper lakes. In all the lakes, however, habitat alterations began with the tributary streams and have been much more conspicuous along the shore and in shallow bays. The entraining effect of the "thermal bar" (Rodgers 1965) — a vertical temperature discontinuity which appears near the shores for up to 2 mo in the springtime — has been identified as a factor which further accentuates the difference between nearshore and offshore water quality (Colby et al. 1972). The littoral areas are vital to most of the main lake species, moreover, so even where the main lake waters appear quite healthy for fish life, quite localized pollution can have effects on stocks which range over broad areas.

The first species to succumb to habitat depreciation apparently was the Atlantic salmon of Lake Ontario (Huntsman 1944). Deforestation of the drainage basin caused reduced flows at critical times for the fish, and made large stretches of streams uninhabitable by reason of increased temperatures and heavy silt burdens. The construction of dams, moreover, blocked spawning migrations. The salmon were in serious difficulty before 1850 and extinct by 1900. Hartman (1972) recorded comparable physical changes in the Lake Erie drainage basin, and in addition drew attention to extensive marsh drainage in the early years of settlement. There were no specific examples of the effects of these changes on the fish stocks, but it is beyond question that the ichthyofauna was affected in important ways. Beeton (1969), Lawrie and Rahrer (1973), and Wells and McLain (1973) similarly noted that the discharge of milling wastes from the lumbering industries of lakes Huron, Michigan, and Superior was extensive in the last century, and suggested that accumulation of these materials in and near the mouths of tributary streams may have had serious effects on reproduction of some species like lake whitefish and lake herring.

The authors of the SCOL lake case histories were all of the view that water quality changes in the main bodies of lakes Superior, Huron, and

Michigan have been of little general importance in the depreciative changes of fish stocks. In lakes Erie and Ontario, however, much attention has been focused in recent years on cultural eutrophication (Beeton 1965) as an obvious and potentially important source of stress for fish stocks. Excessive loading of the waters with plant nutrients (especially N and P) has resulted in proliferation of algae, higher turbidity, altered water color, and depleted hypolimnial oxygen (Colby et al. 1972).

In the extreme, cultural eutrophication can take large expanses of water out of fish production through oxygen depletion, as is apparently the case with the central basin of Lake Erie (Regier et al. 1969; Regier and Hartman 1973). To the extent that suitable alternative habitat is not accessible to resident fish species, stocks can be eliminated. Regier et al. (1969) suggested that in Lake Erie oxygen depletion resulted in concentration and increased mobility of the blue pike and walleye stocks and a consequent increased vulnerability to the fishery.

The biological consequences of cultural eutrophication are far-reaching. Benthic invertebrates are seriously affected, for example. In Lake Erie, the once abundant burrowing mayfly (*Hexagenia*) is now virtually absent (Carr and Hiltunen 1961) and the significance of the loss of this important forage item, although not precisely understood, must have been profound. In the Bay of Quinte, extensive areas of rooted aquatic vegetation have disappeared, presumably as a result of shading by dense algal blooms (Hurley 1973), and loss of forage and cover must have been important to resident fish stocks. Zooplankton species composition changes have also been recorded, and increases in the parasite burdens carried by fish also appear to be characteristic of advanced cultural eutrophication (Colby et al. 1972). Again, the exact consequences of these effects on fish stocks cannot be defined.

The sessile alga *Cladophora* has become increasingly conspicuous along the shores of the lower lakes in recent years, and this has probably also had important effects. On the one hand, when the crops of the alga break off to drift in the lake, the filaments ultimately fragment and sink, to make a fine sediment which could affect the shoreline and shoal spawning areas, where whitefish and lake trout eggs must overwinter (Christie 1973). In Lake Ontario, on the other hand, the presence of the alga has altered the productivity of the limestone reefs substantially. The dense beds of *Cladophora* provide food and shelter for huge populations of the amphipod *Gammarus*, and these in turn attract and perhaps encourage large populations of yellow perch. Perch proliferated in the eastern outlet basin of Lake Ontario after collapse of the whitefish stocks, and it was suggested that improved littoral food supplies may have contributed to this (Christie 1973).

The extent to which eutrophication has encouraged species composition change, by conferring advantage on the species having the best tolerance for polluted water, is a question of considerable interest. In Lake Erie, yellow perch, freshwater drum (*Aplodinotus grunniens*), fathead minnows (*Pimephales promelas*), spottail shiner (*Notropis hudsonius*), and centrarchids, the eggs of which are protected from deoxygenation during development either by pelagic situation, attachment to plants, etc., or aeration by the parent fish, were all considered to have special protection from extreme conditions of eutrophication (Regier et al. 1969). To this list may be added the smelt, whose eggs are sessile, but free from the bottom on short pedicels (Scott and Crossman 1973). To this extent, therefore, the recent dominance of Lake Erie by smelt and perch could reflect the pollution resistance of these species.

In the Bay of Quinte, invasion of the white perch (*Morone americana*) occurred around 1950 (Scott and Christie 1963), and before 1960 the species had assumed dominance (Christie 1973). Since that time the stocks have continued to expand in biomass, apparently at the expense of centrarchid fishes. In spite of similar diets, they evidently have had no major impact on yellow perch (D. A. Hurley personal communication). The success of this invader probably relates to a better tolerance of polluted conditions than that evidenced by the natives, but Christie (1973) argued that the promptness with which proliferation occurred was a reflection of the absence of predators. This argument was based on the contrast between the dominant status and slow growth rate of the species in the Bay of Quinte, and its modest population density and fast growth rate in nearby West Lake. In the latter lake pollution was not as severe and the predators were much more abundant. The inference was that the eutrophic state of the Bay of Quinte, along with heavy fishing pressure, had greatly reduced the abundance of the native piscivores, and thus permitted establishment and dominance of white perch. The consequences of this are poorly understood, but it is hard to see how any of the premium stocks could survive in the Bay of Quinte at present, on account of white perch alone.

The Bay of Quinte is not as highly urbanized as many harbors and bays of Lake Ontario, but its degradation is almost complete (Hurley 1973). The bay no longer appears to be suitable spawning habitat for lake herring and whitefish. The final demise of the Bay of Quinte whitefish can thus be attributed to eutrophication, whether the exact cause related to the direct effects of oxygen depletion or to the indirect effects related to the proliferation of white perch. The consequences, in terms of fish yields from eastern Lake Ontario, were severe.

In recent years there has been a great deal of concern about insidious accruals of chlorinated hydrocarbons (primarily pesticides like DDT), and heavy metals such as mercury. Both kinds of materials are persistent in the system and passed up the food chains, with accumulation. The practical results have been that these materials have in places exceeded levels allowable by health authorities for human consumption, and commercial fisheries have suffered considerable economic loss. One positive result, however, has been that 1973 saw a substantial recovery in western Lake Erie walleye stocks, after several years of fishery restriction because of the high mercury levels (Great Lakes Fishery Commission 1973). The pesticides, on the other hand, are known to inhibit fish reproduction (Burdick et al. 1964). However, the high concentrations evidently occurred after the major fish species changes, and little can be said about population effects. The use of DDT has been restricted for several years, and already the stocks of Lake Michigan salmonids are carrying significantly lower levels of the pesticide (J. F. Carr personal communication). Other known persistent pollutants will likely be restricted, and in time their concentrations in fish flesh will be reduced. New chemical compounds are being constantly produced, however, and it will require a great deal of vigilance to seek out and control them before they cause damage to fish or people.

A kind of habitat deformation about which even less is known, is that of thermal pollution. The proliferation of thermal electricity generating stations around the Great Lakes has been swift over the past 10 yr, and much further expansion is expected. No long-term studies of the direct effects on fish stocks, or of the overall effects of these stations on the heat budget of the lakes, have been completed.

Lake Erie

Regier and Hartman (1973) presented the most recent review of Lake Erie's fisheries, their histories, and man's effects on them, so the following account is cursory. As noted earlier the fishery histories of the four Great Lakes which were originally oligotrophic offer some basis for comparison, but Lake Erie is quite distinctive. Even the native salmonids of its eastern basin could not be expected to respond to stresses in the same way as those of the other lakes because all were at or near the southern limits of their geographic distributions (Scott and Crossman 1973). The large populations of warmwater fishes might also be expected to interact with the salmonids and coregonids in varying degrees. Figure 10 (redrawn from Hartman 1972) shows that the lake herring at least has achieved high levels of abundance in the past. Collapse of these stocks

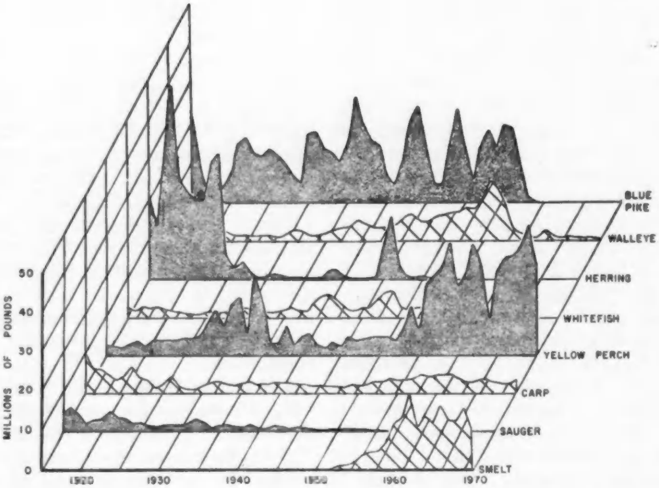


FIG. 10. Commercial landings of important Lake Erie fishes 1915–70 (after Hartman 1972).

in the 1920s in fact was the first of the major recent shocks to affect the Lake Erie fish stocks and fisheries.

The collapses of the blue pike and walleye stocks occurred in the mid- to late 1950s. Of these two it will be noted (Fig. 10) that blue pike was the more important fish to commercial fishermen. Although its fluctuations were wildly erratic since the 1890s, it produced average yields in excess of 4.5 million kg/yr for many years. Parsons (1967) documented the failure of the stock, indicating that the 1954 year-class was the last of any consequence, and that during the terminal years the rates of growth of the remaining fish increased markedly. This latter change is perhaps not too surprising, because the two species collapsed more or less simultaneously, thereby divesting the lake of all its major piscivores, and forage must have been available in excess. Parsons (1970) did not, however, suggest any reasons for the collapse.

The walleye catch increased gradually over a long span of years and its collapse, occurring so quickly after the peak yield of 1956 (6 million kg) was all the more traumatic for the fishery. Here also, Parsons (1970) determined that year-class strength declined sharply after the production of the 1952 year-class, and that the decline was accompanied by sharply increased rates of growth. Unlike that of blue pike, however, the average age of walleye was reduced during the collapse, and this reflected a continued interference by the fishery. Regier et al. (1969) discussed the possible effects of deoxygenation of the central basin, of continually increasing fishing intensity, and of contemporaneous increase of the smelt population on recruitment failure in the walleye stock. Hartman (1972) contrasted the smaller stock of the Eastern Basin with the major stocks of the Western Basin, and felt that although the eutrophication stress was not likely so intense to the east, smelt were an equally significant factor there. He preferred the view that light fishing intensity to the east could be credited for persistence and apparent stability of this stock. This view has received recent support. As noted above, sale of walleye has been restricted for several years because of excessive levels of mercury in the flesh, and in 1973 there were reports of substantial recovery in the western basin (Great Lakes Fishery Commission 1973).

The increases in yellow perch and smelt yield without question reflect real abundance increases. The perch catches had been especially erratic in recent years, and Hartman (1972) expressed concern for the future of the stocks. He noted also that large perch year-classes were synchronous with walleye year-classes and that reproductive success of both species seemed to be influenced by springtime temperature conditions.

The role of smelt is not understood. Collapse of blue pike may have been related to population increase in smelt, but certainly overfishing and eutrophication effects can also be indicted. Collapse of the lake herring in the 1920s may more likely be a simple result of overfishing, as no preceding stock shifts could be associated. This was the view of Van Oosten (1930). Environmental stresses, however, cannot be altogether ruled out, at least as collateral factors. Figure 10 shows an increase in yellow perch catches in the years following the blue pike collapse, and Regier et al. (1969) inferred that this reflected a response of the perch stocks to food resources freed by decline of the blue pike.

Discussion

That the elimination of lake trout and burbot triggered essentially similar events in the main bodies of all the oligotrophic lakes suggests that habitat degradation (although clearly not altogether innocent of blame in the lower lakes) was not as important as overfishing and the appearance of new species. The consensus to this effect must be considered an important outcome of the SCOL Symposium, in that it permits a new optimism (if somewhat guarded) about the future of the Great Lakes fisheries. In the lower lakes the evidence of depreciation of water quality has been manifest for a long time, and separate effects of pollution and overfishing could not always be distinguished. This led to a tendency to treat all fishery problems of all the lakes as though they originated with environmental change, either natural or otherwise. This direction was thought to be the only appropriate one, because where there were doubts about the reasons underlying the difficulties of any fish stock, it was obviously unwise to tamper with the economics of a fishery to remedy the problem. This, in effect, perpetuated the system of unregulated fisheries. This was effectively nonmanagement, and the optimism now is simply that some kinds of management may be possible. This view has been fortified by positive results obtained through sea lamprey control and salmonid stockings, and, not least, encouraged by the knowledge that the fisheries are now so severely depressed that restrictive management practices are probably economically possible in the present circumstances.

The prompt shifts in abundance of yellow perch, deepwater ciscoes, alewife, and smelt, in most cases suggested that these stocks could increase quickly to utilize available space and forage surpluses in the system. This did not, however, appear the case in Lake Huron recently, where whitefish, ciscoes, smelt, and alewife all reached low levels of abundance. The Saginaw Bay fishery compensated somewhat for the loss of the ciscoes by shifting effort to yellow perch, but elsewhere in the lake the fisheries have lost their broad base of support, and persist only as localized operations where whitefish fishing is still possible. The impression is therefore that no fish species of commercial size has filled the void.

The situation in Lake Ontario is not entirely analogous, in that the lake still supports large stocks of alewife and smelt. The abyss of the lake, however, is effectively unoccupied during the summer, when alewife stocks are inshore. The bottom at medium depths is densely populated by slimy sculpins (*Cottus cognatus*) (Christie 1973), and the invertebrates *Mysis* and *Pontoporeia* are both in high abundance lake-wide (Hiltunen 1969). Recent work with midwater trawling gear (W. J. Christie unpublished data) found smelt and alewife in appreciable numbers, living pelagically in the middle and upper waters from close to shore to regions of great depth.

The summertime absence of fish in the deep parts of the hypolimnion raises a question concerning the efficiency of a system dominated by alewife and smelt. Possibly more nutrient materials reach the bottom than would be the case if the invertebrates entered a major fish food web. The winter migration of alewife to the abyss of the lake (Wells 1968) must involve little demand on the system. It may also be true that total productivity was augmented in some degree by transport of materials through the system by the wide-ranging piscivores lake trout and burbot, and, if true, the pelagic inshore–offshore movements of smelt and alewife in summer can scarcely be as effective a vectoring system as the historical lateral and vertical coverage afforded by the piscivores and ciscoes. The concept of a coherence in the flow of energy and materials in a lake system, is implicit in the work of Ryder (1965). In that study fish yield was found proportional to average depth and an edaphic factor (total dissolved solids), for a large series of north temperate zone lakes.

The variance of Ryder's (1965) regression was very large. R. A. Ryder (personal communication) notes, however, that the lakes varied with respect to level of fishing intensity and yet there was no evidence that yield levels were higher in those lakes where the fisheries depended on stocks of fish at lower trophic levels. This generalization is illustrated further in Table 4 and Fig. 10, even though the yield changes have clearly been influenced to some extent by the availability of alternative merchantable species, and the abilities of the fisheries to develop effective means to capture them. This phenomenon might have a metabolic basis of the sort discussed by Kerr and Martin (1970) or some other as yet unidentified basis, but there is the possibility that the shorter food chains in the heavily fished (or heavily polluted) lakes do not produce higher yields than the original systems did, simply because the new species arrays are not ecologically able to fully exploit the resources of the lake. This is an area which deserves intensive investigation. The Ryder (1965) model itself deserves further attention because with validation and refinement it could become a valuable predictive tool. Used simply as an analytical device, however, it has immediate usefulness.

Regardless of the reasons for the apparent independence of yield from the trophic level attacked by any fishery, the practical significance of the observation is that fishery administrators must now recognize that the Great Lakes commercial fisheries gain no yield benefits by fishing stocks at lower trophic levels, and in fact stand to gain a great deal economically by harvesting high-valued fish like lake trout and whitefish rather than low-priced fish like yellow perch. This should be a compelling inducement to make all possible effort to rehabilitate the premium fishes wherever possible. A further strong inducement lies with the burgeoning demands for recreational fishing opportunities in the Great Lakes area. Angling fisheries for large salmonids like those recently developed by the State of Michigan have the potential for even greater social and economic benefits than the commercial fisheries.

The loss of the fourhorn sculpin (*Myoxocephalus quadricornis*) from Lake Ontario was a particularly anomalous event in the series of observations. It was an important trout and burbot forage species (Dymond 1928), and ranged out to the extreme depths of Lake Ontario. Their decline occurred during the 1950s after predation pressure had been removed, and it cannot be explained on the basis of present information. Knowledge of the life history is incomplete, and study of its ecology in the Great Lakes is urgently needed. This can be stated as a general indictment of past fisheries research, which was almost invariably oriented to economically important species.

The evidence examined here has suggested that the sea lamprey, the alewife, and the smelt have all exhibited population changes like those of newly introduced insect or other animal pests (Elton 1958), i.e. they have exploded to apparently excessive levels of abundance and then receded. The white perch appears an exception in that its commercial abundance has continued to increase since its colonization in Lake Ontario. In Oneida Lake it went through the more typical cycle of explosion and decline (J. Forney personal communication) and this may suggest that the continuing degradation of the water in the Bay of Quinte is somehow interfering with any natural controls which would normally contain the species.

The point has not been adequately investigated, but what little evidence is available suggests that the sometimes long time lags between first appearance of the exotic fish described here and their proliferations, were periods of virtually no population increase, following which they then exploded during a few generations. The rate at which colonization occurs in terrestrial insect invaders, on the other hand, appears to proceed exponentially from the time of first appearance (Elton 1958). Timing of the release in the fish cases evidently related to predator abundance at arrival, and this may be the situation with many terrestrial invaders as well. In any case, the suggestion that delays in establishment of parasite cycles in the new habitat (along with such other factors as acceptance as forage by native predators) raised by Elton (1958) and others in explanation of the postinvasion overpopulations, apparently does not apply in the case of the fish.

There are few indications, in the data examined here, of distinctions between the responses of native species and exotics, when relieved of predation pressure. One possible difference noted was in the degree of population increase. The alewife in Lake Michigan rose to assume dominance of the entire lake in a very few years, whereas native species like yellow perch and ciscoes have not undergone such extreme increases. A generalized postulate about invaders is that they may at least temporarily lose some of their specialized habitat requirements in totally new surroundings, and are thus able to proliferate further than native stocks which are relieved of predation, but still subject to other ecological constraints. A possible support for this was seen among the cases examined, in that a predator stock decline did not need to be extreme to permit the intrusion of a new species. The alewife colonized Lake Ontario during a period when lake trout stocks were declining, but still at relatively high levels of density. This was also true of the colonization of Lake Michigan by smelt. Clearly, if piscivore stock declines are sufficient to make their natural forage superabundant, this must relieve predation on the invader, and evidently it requires only a small advantage of this sort to allow establishment. The native yellow perch stocks in Lake Erie, Lake Ontario, and Saginaw Bay (Baldwin and Saafeld 1962), all underwent sharp increases. These changes occurred after rather extreme alterations in the biotic environment in each case, and this supports the postulate. Even if there were strong data to measure the relative plasticity of natural and exotic species, however, it is unlikely such information would be useful to predict the ease with which future invaders could intrude themselves into the lake systems. Such factors as biotic potential and degree of spawning habitat stereotype would almost certainly vary from one invading species to another.

In practical terms, the difference between ascendency of a native and an exotic species is rather important. First, control measures to check the increase of a pest fish will inevitably be expensive and be applied too late. The case of the sea lamprey was a simple one, in which the life history is such as to permit the destruction of a number of year-classes of ammocoetes in a stream at one time. The method was developed too late to save the lake trout stocks, and it is a reasonable prediction that control of lake-dwelling pests will be even more difficult, if not altogether impossible, to develop. Secondly, if the pests equilibrate, with or without special control measures, their presence will often prove to be an additional cost to the yield potential of the lake.

Smith (1968, 1972) has referred to the invading species as marine invaders. Aside from the fact that the term does not apply to all the Great Lakes exotic species, I dispute its use on the grounds that it implies that the marine species have some special powers in respect to ability to disrupt a freshwater system, or that species of marine origin represent the only threats for the future. The recent report of the occurrence of the Chinese Mitten crab (*Eriocheir sinensis*) in Lake Erie (Nepszy and Leach 1973) illustrates the fact that the potential for introduction of exotic invertebrates must be great. Growth of the aquarium hobby has similarly increased the threat of release of pest fishes.

The models of Regier and Loftus (1972) and Colby et al. (1972) similarly identify osmerids and clupeids as components of the sequences of species to be expected as results of the "fishing-up" process and eutrophication, respectively. These models accurately reflect past events, but I maintain that they hold no key for predicting the course of future events. This is because, first, as noted above, lake fish productivity may be influenced by the unknown life histories and distributions of future exotics. Secondly, yield is influenced by the catchability and usefulness of the pest. In fact, the only prediction about the future invaders based on present information, is that they will likely always be smaller in size than the prevalent species in the commercial catch, because of the pressure of fishing effort.

The foregoing passages can be summarized by the judgment that at this stage in our knowledge we must accept that instability can facilitate the appearance of new pests, or the recurrence of outbreaks of either native or previously introduced species. The only recognizable defense against pest outbreaks, in other words, is to maintain a relatively stable predator–prey balance.

In the present context, stability refers to the tendency of fish species populations in a community to maintain position relative to one another, and it is synonymous with ecosystem homeostasis (Odum 1971). Stock oscillations over long time periods as reflected in the yields of species such as the Lake Erie blue pike suggest that in some cases stability prevailed in spite of extreme variations in the densities of component stocks in the community. The communities of oligotrophic lakes exhibited less extreme short-term variation in their component stocks but here also it must be inferred that each of the native species was well adapted to retain its niche. The critical levels beyond which competitive advantage is lost have not been measured for any Great Lakes fish stock and, as in the past, the high levels of natural variability will continue to pose problems for future studies. Determining yield levels appropriate to maintaining stability, however, will be the central problem area for applied research in the future.

The implications of this sort of preventive management are profound, for both research and management. First, it would have to be recognized that allowable yields would have to be appreciably lower than heretofore. Next, the means of monitoring the systems would have to be substantially improved, and it is not at all clear how this could be done, for the various reasons given earlier. The conventional statistics are unreliable when the fishery changes its target species, or where the statistical areas are too large to detect progressive loss of individual stocks. More important, species of no economic, but possibly great biological, significance are not monitored regularly.

From the standpoint of research, the problems are equally difficult. In the past the difficulties involved in estimating sustainable yields for individual species populations have been insurmountable, and now the magnitude of the task of learning how to manage whole communities is almost dismaying. It was a major lesson of the SCOL series of papers that traditional studies in aquatic ecology which are paced to the durations of the life cycles of the organisms, are too slow to cope with the dynamics of the complex freshwater systems.

As noted above, conventional studies of homeostasis and interspecies reactions are still needed, but their scope and intensity must be greatly increased. The unsolved problems of sampling to measure the food habits of such enormous stocks as those of the smelt must be approached with new and greater vigor. In addition to their failure to measure adequately the real consumption rates in the past, such studies were limited to the extent that they could not be accompanied by estimates of the biomass of either predator or prey, or of competitors and their common food resource. This problem underlies the question of yield estimates as well. Past studies have only rarely been able to estimate current harvest rates, much less predict allowable yields. Relative abundance estimates have been used effectively in some studies, but the catch of one species taken by a particular sampling gear cannot be related to the catch of another species caught by different gear. Catch and effort approaches to population estimation (Beverton and Holt 1957; Ricker 1958 etc.) appear to be too slow and retrospective for dynamic systems like those of the Great Lakes. Fish tagging studies may yet hold some promise, but it may be years before procedures are developed which are applicable to the smaller and more fragile species. The most promising approach at present involves the use of echo sounders. Studies in their application to fish census are currently underway at the University of Wisconsin, the U.S. Bureau of Sport Fisheries and Wildlife, and the Canada Centre for Inland Waters, to mention only those institutions directly involved with the Great Lakes.

The general approach which recommends itself as the one most likely to yield ecological understanding and the earliest rehabilitation of the lakes is termed experimental management. This would involve the conventional management approaches like regulation and salmonid stocking, but would require that they be applied as carefully designed experiments which would measure perturbation of the systems.

The foregoing prescription for approaching the problems of the Great Lakes fisheries is somewhat at odds with that of Regier (1974). In his more generalized review of the state of fish ecology, Regier interpreted the observed depreciation of freshwater fish stocks in terms of a "general stress syndrome." In his view, the stresses of excessive fishing and/or pollution work to force the ecosystems towards dominance by smaller and more pelagic forms in a way that may ultimately be predictable. My view, again, is that the sequence of invasion by, and habitat requirements for, future possible pest species is not predictable, and therefore the trends in yield cannot be expected to take any particular pattern in a stress progression.

Regier's (1974) paper is effectively a plea for balance and integration between the holistic and reductionistic approaches. I endorse this emphatically, but Regier asks for greater emphasis on holism. I fear the balance can be very readily tipped in this direction, however, because of the growing interest among fisheries biologists in the potentially greater conceptual strength of holism. It is an additional danger that holism superficially appears to offer short-cut and cheaper means of attaining the goals of fisheries management and this could influence budget priorities if misunderstood by administrators. Present holistic models have very weak resolution and further refinement depends heavily on reductionistic studies.

The SCOL symposium both demonstrated the value of long-term observational series however limited in scope, and emphasized the deficiencies of those series which had inadequate scope. The biological survey approach is therefore not only essential to future work but must be extended and intensified. It is appropriate to use an ecological classification of fish "professions" for modelling, but in this work I have tried to emphasize the deficiencies in our understanding of homeostasis, of materials vectoring, and of the roles of the economically unimportant species in the Great Lakes systems, and such understanding cannot be achieved without resort to conventional taxonomy. In a sense, the method of iterative refinement of a community model espoused by Regier (1974) is essentially the same as the method of induced artificial perturbations described here. The latter also requires a general community model which can be modified according to the results of consecutive management experiments, but it has the advantages of potentially greater efficiency, and possibly predictable timetable.

A possible criticism of the proposed dualistic approach is that the costs of intensive ecological research of this sort will be prohibitive. Higher research budgets are assuredly indicated, but great economies can be effected by coordinated application of existing resources. In both the United States and Canada, there are large numbers of university scientists engaged in both long- and short-term studies of fish stocks; there are two large government fisheries research agencies; and nearly every state and the Province of Ontario has management fisheries biologists engaged in stock monitoring activities. Biologists from the private sector, from universities, and government agencies are engaged in extensive work in physical limnology and subvertebrate biology in connection with thermal and other pollution impacts on Great Lakes water quality. Several museums maintain fish collections from the Great Lakes. The ichthyologists have not typically become involved in the dynamics of short-run fish species change, but the total number of scientific personnel in the other groups is very large, and if their efforts were coordinated, certainly ecological theory and practice could advance apace.

Regier (1974) expresses concern that the modern trend towards a team approach in systems ecology and management planning will result in a loss of scientific freedom and loss of those scientists who cannot function in a team. In my view there is a danger of encouraging scientific mediocrity as well. In pointing out the resources available I do not imply that such team work is necessary. Given general agreement on scientific goals and sufficient communication, it must be possible to maximize the rate of progress without interfering with individuality.

Readers from outside the community of Great Lakes fishery workers will probably have been puzzled by the optimism of the foregoing passages, in the face of known rate of change in the quality of Great Lakes water (Beeton 1965). It must be admitted that if past trends continue there is no long-term hope for oligotrophic-type fish communities, even though we have very limited evidence that cultural eutrophication and other kinds of pollution have affected fish stocks fo far. Present indications are, however, that both the U.S. and Canada view seriously the need to restore water quality in the Great Lakes. I believe this dedication will soon bring about action and planners will agree with fishery scientists that the best long-term index of the health of the Great Lakes, is a healthy and well-balanced fish community.

Acknowledgments

I thank my colleagues H. H. Harvey, W. T. Geiling, D. A. Hurley, H. A. Regier, W. A. Hartman, K. H. Loftus, A. H. Berst, L. Wells, and A. H. Lawrie for reviewing the manuscript and contributing many helpful suggestions.

ABROSOV, U. N. 1969. Determination of commercial turnover in natural bodies of water. *In* Problems of ichthyology. (Transl. from Russian by Am. Fish. Soc. 9: 482–489)

ANDERSON, E. D., AND L. L. SMITH JR. 1971. Factors affecting abundance of Lake Herring (*Coregonus artedii* Lesueur) in western Lake Superior. Trans. Am. Fish. Soc. 100: 691–707.

APPLEGATE, V. C., J. H. HOWELL, J. W. MOFFETT, B. G. H. JOHNSON, AND M. A. SMITH. 1961. Use of 3-trifluormethyl-4-nitrophenol as a selective sea lamprey larvicide. Great Lakes Fish. Comm. Tech. Rep. No. 1: 35 p.

BALDWIN, N. S. 1948. The American smelt, *Osmerus mordax* (Mitchill), of South Bay, Manitoulin Island, Lake Huron. Trans. Am. Fish. Soc. 77: 176–180.

1968. Sea lamprey in the Great Lakes. Limnos 1: 20–27.

BALDWIN, N. S., AND R. W. SAALFELD. 1962, plus supplement 1970. Commercial fish production in the Great Lakes, 1867–1960. Great Lakes Fish. Comm. Tech. Rep. No. 3: 166 p.

Beeton, A. M. 1965. Eutrophication of the St. Lawrence Great Lakes. Limnol. Oceanogr. 10: 240–254.

1969. Changes in the environment and biota of the Great Lakes, p. 150–187. *In* Eutrophication: causes, consequences, correctives. Nat. Acad. Sci., Washington, D.C.

Beeton, A. M., and W. T. Edmondson. 1972. The eutrophication problem. J. Fish. Res. Board Can. 29: 673–682.

Berst, A. H., and G. R. Spangler. 1972. Lake Huron: effects of exploitation, introductions, and eutrophication on the salmonid community. J. Fish. Res. Board Can. 29: 877–887.

1973. Lake Huron: The ecology of the fish community and man's effects on it. Great Lakes Fish. Comm. Tech. Rep. No. 21: 41 p.

Berst, A. H., and A. A. Wainio. 1967. Lamprey parasitism of rainbow trout in southern Georgian Bay. J. Fish. Res. Board Can. 24: 2539–2548.

Beverton, R. J. H., and S. J. Holt. 1957. On the dynamics of exploited fish populations. Minist. Agric. Fish. Food. Fish. Invest. London (Ser. II) XIX: 532 p.

Budd, J. C., F. E. J. Fry, and P. S. M. Pearlstone. 1969. Final observations on the survival of planted lake trout in South Bay, Lake Huron. J. Fish. Res. Board Can. 26: 2413–2424.

Burdick, G. E., E. J. Harris, H. J. Dean, T. M. Walker, J. Skea, and D. Colby. 1964. The accumulation of DDT in lake trout and the effect on reproduction. Trans. Am. Fish. Soc. 93: 127–136.

Carr, J. F., and J. K. Hiltunen. 1961. Changes in the bottom fauna of western Lake Erie from 1930 to 1961. Limnol. Oceanogr. 10: 551–569.

Christie, W. J. 1963. Effects of artificial propagation and the weather on recruitment in the Lake Ontario whitefish fishery. J. Fish. Res. Board Can. 20: 597–646.

1968. Possible influences of fishing in the decline of Great Lakes fish stocks, p. 31–38. *In* Proc. 11th Conf. Great Lakes Res., Int. Assoc. Great Lakes Res.

1972. Lake Ontario: effects of exploitation, introductions, and eutrophication on the salmonid community. J. Fish. Res. Board Can. 29: 913–929.

1973. A review of the changes in the fish species composition of Lake Ontario. Great Lakes Fish. Comm. Tech. Rep. No. 23: 65 p.

Christie, W. J., J. M. Fraser, and S. J. Nepszy. 1972. Effects of species introductions on salmonid communities in oligotrophic lakes. J. Fish. Res. Board Can. 29: 969–973.

1974. Effects of the sea lamprey (*Petromyzon marinus*) on Lake Ontario fish stocks. File report. Glenora Fish. Sta., Glenora, Ont.

Christie, W. J., and H. A. Regier. 1973. Temperature as a major factor influencing reproductive success of fish — two examples. Rapp. P-V Reun. Cons. Perm. Int. Explor. Mer 164: 208–218.

Colby, P. J., G. R. Spangler, D. A. Hurley, and A. M. McCombie. 1972. Effects of eutrophication on salmonid communities in oligotrophic lakes. J. Fish. Res. Board Can. 29: 975–983.

Coleman, A. P. 1922. Glacial and post-glacial lakes in Ontario. Univ. Toronto Stud. Biol. Ser. No. 21: 1–76.

Cucin, D., and H. A. Regier. 1966. Dynamics and exploitation of lake whitefish in southern Georgian Bay. J. Fish. Res. Board Can. 23: 221–274.

Deason, H. J. 1939. The distribution of cottid fishes in Lake Michigan. Pap. Mich. Acad. Sci. Arts Lett. No. 24: 105–115.

Dymond, J. R. 1928. Some factors affecting the production of lake trout (*Cristivomer namaycush*) in Lake Ontario. Univ. Toronto Stud. Biol. Ser. No. 31: 29–41.

1932. Records of the alewife and steelhead (rainbow) trout from Lake Erie. Copeia 1932: 32–33.

Dymond, J. R., J. L. Hart, and A. L. Pritchard. 1929. The fishes of the Canadian waters of Lake Ontario. Univ. Toronto Stud. Biol. Ser. No. 33: 1–35.

Elton, C. 1958. The ecology of invasions by animals and plants. Methuen, London. 181 p.

El-Zarka, S. E. D. 1959. Fluctuations in the population of yellow perch, *Perca flavescens* (Mitchill), in Saginaw Bay, Lake Huron. U.S. Fish Wildl. Serv. Fish Bull. 59: 365–415.

Fry, F. E. J. 1953. The 1944 year class of lake trout in South Bay, Lake Huron. Trans. Am. Fish. Soc. 82: 178–192.

Fry, F. E. J., and K. E. F. Watt. 1957. Yields of year classes of the smallmouth bass hatched in the decade of 1940 in Manitoulin Island waters. Trans. Am. Fish. Soc. 85: 135–143.

Graham, J. J. 1956. Observations on the alewife, *Pomolobus pseudoharengus* (Wilson), in fresh water. Univ. Toronto Stud. Biol. Ser. No. 62: 1–43.

Great Lakes Fishery Commission. 1973. Annual Report. Ann Arbor, Mich.

Harkness, W. J. K., and J. R. Dymond. 1961. The lake sturgeon. The history of its fishery and problems of conservation. Ont. Dep. Lands For. Fish Wildl. Br. 121 p.

Hartman, W. L. 1972. Lake Erie: effects of exploitation, environmental changes, and new species on the fishery resources. J. Fish. Res. Board Can. 29: 899–912.

1973. Effects of exploitation, environmental changes, and new species on the fish habitats and resources of Lake Erie. Great Lakes Fish. Comm. Tech. Rep. No. 22: 43 p.

Hile, R. 1937. The increase in the abundance of the yellow pike-perch, *Stizostedion vitreum* (Mitchill) in Lakes Huron and Michigan, in relation to the artificial propagation of the species. Trans. Am. Fish. Soc. 66: 143–159.

Hile, R., P. H. Eschmeyer, and G. F. Lunger. 1951. Status of the lake trout fishery in Lake Superior. Trans. Am. Fish. Soc. 80: 278–312.

Hiltunen, J. L. 1969. The benthic macrofauna of Lake Ontario, p. 39–49. *In* Limnological survey of Lake Ontario, 1964. Great Lakes Fish. Comm. Tech. Rep. No. 14.

HUBBS, C. L., AND K. F. LAGLER. 1958. Fishes of the Great Lakes region. Univ. Michigan Press, Ann Arbor, Mich. 213 p.

HUNTSMAN, A. G. 1944. Why did Ontario salmon disappear? Trans. R. Soc. Can. (Ser. 3) 38 (V): 83–102.

HURLEY, D. A. [Chmn.] 1973. First Annual Report of Project Quinte for 1972. Glenora Fish. Sta. 30 p.

KERR, S. R., AND N. V. MARTIN. 1970. Trophic-dynamics of lake trout production systems, p. 365–376. *In* J. H. Steele [ed.] Marine food chains Oliver and Boyd, Edinburgh.

KOELZ, W. 1926. Fishing industry of the Great Lakes. U.S. Dep. Commer. Bur. Fish. Doc. No. 1001: 554–617.

LARK, J. G. 1973. An early record of sea lamprey from Lake Ontario. J. Fish. Res. Board Can. 30: 131–133.

LAWRIE, A. H. 1970. The sea lamprey in the Great Lakes. Trans. Am. Fish. Soc. 99: 766–775.

LAWRIE, A. H., AND J. F. RAHRER. 1972. Lake Superior: effects of exploitation and introductions on the salmonid community. J. Fish. Res. Board Can. 29: 765–776.

1973. Lake Superior: A case history of the lake and its fisheries. Great Lakes Fish. Comm. Tech. Rep. No. 19: 69 p.

MACCALLUM, W. R., AND H. A. REGIER. 1970. Distribution of smelt, *Osmerus mordax*, and the smelt fishery in Lake Erie in the early 1960s. J. Fish. Res. Board Can. 27: 1823–1846.

MACKAY, H. H. 1934. Record of the alewife from Lake Huron. Copeia 1934: 97.

MCCOMBIE, A. M., AND F. E. J. FRY. 1960. Selectivity of gill nets for lake whitefish, *Coregonus clupeaformis*. Trans. Am. Fish. Soc. 89: 176–184.

MILLER, R. R. 1957. Origin and dispersal of the alewife, *Alosa pseudoharengus*, and the gizzard shad, *Dorosoma cepedianum*, in the Great Lakes. Trans. Am. Fish. Soc. 86: 97–111.

MOFFETT, J. W. 1957. Recent changes in the deepwater fish populations of Lake Michigan. Trans. Am. Fish. Soc. 86: 393–408.

1958. Attack on the sea lamprey. Mich. Conserv. 27(3): 21–27.

NEPSZY, S. J., AND J. H. LEACH. 1973. First records of the Chinese mitten crab, *Eriocheir sinensis*, (Crustacea: Brachyura) from North America. J. Fish. Res. Board Can. 30: 1909–1910.

ODUM, E. P. 1971. Fundamentals of Ecology. 3rd ed. W. B. Saunders Co., Toronto, Ont. 574 p.

PALOHEIMO, J. E. 1961. Studies on estimation of mortalities. I. Comparison of a method described by Beverton and Holt and a new linear formula. J. Fish. Res. Board Can. 18: 645–662.

PARSONS, J. W. 1967. Contributions of year-classes of blue pike to the commercial fishery of Lake Erie, 1943–59. J. Fish. Res. Board Can. 24: 1035–1066.

1970. Walleye fishery of Lake Erie in 1943–62 with emphasis on contributions of the 1942–61 year-classes. J. Fish. Res. Board Can. 27: 1475–1489.

PRITCHARD, A. L. 1929. The alewife (*Pomolobus pseudoharengus*) in Lake Ontario. Univ. Toronto Stud. Biol. Ser. No. 38: 37–54.

1931. Taxonomic and life history studies of the ciscoes of Lake Ontario. Univ. Toronto Stud. Biol. Ser. No. 41: 1–78.

RADFORTH, I. 1944. Some considerations on the distribution of fishes in Ontario. Contrib. R. Ont. Mus. Zool. No. 25: 116 p.

REGIER, H. A. 1974. Ecology of fish: A sketch of the state of the science and of its application. Mitt. Int. Verein Limnol. (In press)

REGIER, H. A., V. C. APPLEGATE, AND R. A. RYDER. 1969. The ecology and management of the walleye in western Lake Erie. Great Lakes Fish. Comm. Tech. Rep. No. 15: 101 p.

REGIER, H. A., AND W. L. HARTMAN. 1973. Lake Erie's fish community: 150 years of cultural stresses. Science 180: 1248–1255.

REGIER, H. A., AND K. H. LOFTUS. 1972. Effects of fisheries exploitation on salmonid communities in oligotrophic lakes. J. Fish. Res. Board Can. 29: 959–968.

RICKER, W. E. 1958. Handbook of computations for biological statistics of fish populations. Bull. Fish. Res. Board Can. 119: 300 p.

RODGERS, G. K. 1965. The thermal bar in the Laurentian Great Lakes. Great Lakes Res. Div. Univ. Mich. Publ. No. 13: 358–363.

RYDER, R. A. 1965. A method for estimating the potential fish production of north-temperate lakes. Trans. Am. Fish. Soc. 94: 214–218.

1972. The limnology and fishes of oligotrophic glacial lakes in North America (about 1800 A.D.). J. Fish. Res. Board Can. 29: 617–628.

SCOTT, W. B. 1951. Fluctuations in abundance of the Lake Erie cisco (*Leucichthys artedi*) population. Contrib. R. Ont. Mus. Zool. No. 32: 41 p.

SCOTT, W. B., AND W. J. CHRISTIE. 1963. The invasion of the lower Great Lakes by the white perch, *Roccus americanus* (Gmelin). J. Fish. Res. Board Can. 20: 1189–1195.

SCOTT, W. B., AND E. J. CROSSMAN. 1973. Freshwater fishes of Canada. Bull. Fish. Res. Board Can. 184: 966 p.

SMITH, S. H. 1964. Status of the deepwater cisco population of Lake Michigan. Trans. Am. Fish. Soc. 93: 155–163.

1968. Species succession and fishery exploitation in the Great Lakes. J. Fish. Res. Board Can. 25: 667–693.

1970. Species interactions of the alewife in the Great Lakes. Trans. Am. Fish. Soc. 99: 754–765.

1972a. Factors of ecologic succession in oligotrophic fish communities of the Laurentian Great Lakes. J. Fish. Res. Board Can. 29: 717–730.

1972b. The future of salmonid communities in the Laurentian Great Lakes. J. Fish. Res. Board Can. 29: 951–957.

STONE, U. B. 1947. A study of the deepwater cisco fishery of Lake Ontario with particular reference to the bloater *Leuchichthys hoyi* (Gill). Trans. Am. Fish. Soc. 74: 230–249.

TAIT, J. S. 1970. A method of selecting trout hybrids (*Salvelinus fontinalis* × *S. namaycush*) for ability to retain swimbladder gas. J. Fish. Res. Board Can. 27: 39–45.

VAN OOSTEN, J. 1930. The disappearance of the Lake Erie cisco — a preliminary report. Trans. Am. Fish. Soc. 60: 204–214.

1937. The dispersal of the smelt, *Osmerus mordax* (Mitchill), in the Great Lakes region. Trans. Am. Fish. Soc. 66: 160–171.

1947. Mortality of smelt, *Osmerus mordax* (Mitchill), in Lakes Huron and Michigan during the fall and winter of 1942–1943. Trans. Am. Fish. Soc. 74: 310–337.

1949. A definition of depletion of fish stocks. Trans. Am. Fish. Soc. 76: 283–289.

WELLS, L. 1968. Seasonal depth distribution of fish in southeastern Lake Michigan. U.S. Fish Wildl. Serv. Fish. Bull. 67: 1–15.

1970. Effects of alewife predation on zooplankton populations in Lake Michigan. Limnol. Oceanogr. 15: 556–565.

WELLS, L., AND A. MCLAIN. 1972. Lake Michigan: effects of exploitation, introductions, and eutrophication of the salmonid community. J. Fish. Res. Board Can. 29: 889–898.

1973. Lake Michigan: Man's effects on native fish stocks and other biota. Great Lakes Fish. Comm. Tech. Rep. No. 20: 55 p.

Crustacean Plankton Communities of 340 Lakes and Ponds in and near the National Parks of the Canadian Rocky Mountains[1]

R. STEWART ANDERSON

Department of the Environment
Canadian Wildlife Service
Biology Department, University of Calgary, Calgary, Alta.

ANDERSON, R. S. 1974. Crustacean plankton communities of 340 lakes and ponds in and near the National Parks of the Canadian Rocky Mountains. J. Fish. Res. Board Can. 31: 855–869.

The crustacean plankton communities of 340 lakes and ponds in southern Alberta and southeastern British Columbia were examined. The waters are situated between 660 m and 2455 m in elevation, have areas from <0.1 to 3940 hectares, and range from 0.5 m to 136 m in depth. They represent a wide range of salinities, from 2 ppm to 29,800 ppm. The communities were grouped into seven main types on the basis of the copepod species present. Of the 97 crustacean species present, 32 were copepods, 50 were cladocerans, and 9 were anostracans. The three most common species accounted for over 25% of the total species occurrences. Only two species were present in more than half the total lakes and ponds. A few species seem to be restricted to highly saline waters, and a few to low salinities, but most inhabited a wide range of aquatic environments. The most frequently occurring and abundant species tolerate a wide range of conditions. These species are also characterized by up to a fivefold variation in generation time. Certain species having restricted distribution patterns appear to be limited by both the chemistry of the water and the heat content. Aspects of species distribution, ecology, and interspecific relationships are discussed.

ANDERSON, R. S. 1974. Crustacean plankton communities of 340 lakes and ponds in and near the National Parks of the Canadian Rocky Mountains. J. Fish. Res. Board Can. 31: 855–869.

Nous avons étudié les communautés planctoniques de crustacés de 340 lacs et étangs du sud de l'Alberta et du sud-est de la Colombie-Britannique. Les eaux sont situées entre 660 et 2455 m d'altitude, ont une étendue de <0.1 à 3940 hectares et varient de 0.5 à 136 m de profondeur. Elles possèdent une gamme étendue de salinités, allant de 2 à 29,800 parties par million. Les communautés ont été groupées en sept catégories principales selon les espèces de copépodes présentes. Des 97 espèces de crustacés présentes, 32 sont des copépodes, 50 des cladocères et 9 des anostracés. Les trois espèces les plus communes sont responsables de plus de 25% de toutes les occurrences d'espèces. Seulement deux espèces sont présentes dans plus de la moitié du nombre total de lacs et étangs. Quelques espèces semblent être limitées à des eaux de haute salinité et quelques-unes à des eaux de faible salinité, mais la plupart habitent une gamme étendue d'habitats aquatiques. Les expèces les plus fréquentes et les plus abondantes tolèrent une gamme étendue de conditions. Ces espèces sont de plus caractérisées par une variation, allant jusqu'à cinq ordre de grandeur, du temps de génération. Certaines espèces ayant une répartition restreinte semblent être limitées par la composition chimique et le contenu calorifique de l'eau. Nous discutons des divers aspects de la distribution, de l'écologie et des relations interspécifiques des espèces.

Accepted December 10, 1973

THE MAIN purpose of this study was to provide sufficient data to characterize the crustacean plankton communities of a large number of lakes and ponds in southern Alberta and southeastern British Columbia. This is a region of Canada for which relatively few such data exist. Although this study was confined primarily to the mountain National Parks in the region, information from many other lakes and ponds was included to broaden distributional and ecological data for certain crustacean species.

---

[1] This paper, part of a special issue that comprises a comprehensive review of Limnology in Canada, was prepared to mark the 19th Congress of the International Association of Limnology (SIL), in Winnipeg, Man., during August 1974.

Printed in Canada (J3246)

There are a few comprehensive surveys of crustacean plankton communities in other regions of Canada and in the United States south of Alberta and British Columbia (e.g. Brandlova et al. 1972; Carl 1940; Carter 1971; Mayhood et al. 1973; Patalas 1964, 1971; Patalas and Salki 1973; Pennak 1955; Reed 1962, 1964; Reed and Olive 1956; Rigler and Langford 1967; Whittaker and Fairbanks 1958). Some are out of date, give inadequate basic physical–chemical data, or are not representative of a broad spectrum of the lakes and ponds in an area. Only a few limited studies of crustacean plankton communities or certain groups of crustaceans have been done in the region covered by this study (e.g. Anderson 1968, 1971b; Bajkov 1929; Hartland-Rowe 1965; Rawson 1953; Reed 1959). A review of these and other regional survey studies reveals gaps in our knowledge of the geographical distribution, ranges of environmental tolerances, and basic ecology of many planktonic crustacean species.

This study was conducted in conjunction with inventories of aquatic organisms, sport-fish management projects, and basic research being conducted in lakes and streams in the western Canadian National Parks by the Limnology Unit of the Canadian Wildlife Service for the National and Historic Parks Branch. Few lakes from the north-central foothills region and the southeast corner of Alberta could be included in the survey at this time. As no previous studies have been published for most lakes and ponds of this study, it was necessary to devote much of the available space to basic description.

Methods

Plankton samples were collected during daylight hours with a conical plankton net (mouth diam 25 cm) made of bolting silk (aperture 65–70 μ) towed at approximately 0.5 m/s. For purposes of discussion, "crustacean plankton" refers to all crustacean species collected in the plankton nets except ostracodes, which have been thoroughly treated elsewhere (Delorme 1971). In most lakes and ponds, two or more vertical tows were made from lake bottom to surface from a boat over the deepest area. These collections were supplemented in most cases by surface tows and near-shore tows, either from behind the boat or from shore. Some small ponds were adequately sampled from shore where a weighted plankton net could be thrown 15–20 m. In some lakes, plankton trap samples were collected from specific depths at intervals throughout the 24-h day, both for assessing vertical distribution and for determining plankton net efficiency. Of the 340 lakes and ponds, approximately half were sampled more than once, and 25 were sampled 10 or more times.

Plankton densities reported here have been corrected to account for net inefficiency as indicated elsewhere (Anderson 1970a). The scale of abundance (animals per liter) used in the tabulated results is by order of magnitude (density levels):

1 = <0.1
2 = 0.1–1
3 = 1–10
4 = 10–100
5 = 100–1000

The numbers of crustacean plankters per liter given in Table 2–8 are the highest mean numbers found in the water column on a sampling date in each lake or pond. Occasionally in the tables, the relative abundance figures seem to exceed the total reported. This is because maxima for different species may have occurred on different dates. This was especially true for many prairie sites, such as Church's Pond B (Donald 1971).

To estimate maximum annual heat content for lakes and ponds having such a wide range of depths, I used the mean heat content per liter for the entire water column near the deepest spot at the highest determined temperature, rather than the heat content per cm^2 for the upper 25 m (Patalas 1969, 1972). Zero Celsius was used as the base line. Heat values (Table 2–8) are comparable to the others cited if multiplied by 2.5.

Detailed chemical analyses for most of these waters were performed by the Water Resources Branch, Environment Canada, Calgary. The pH was usually determined in the field. Color (Hazen units; 0 for most of these waters) seemed to have no bearing on distribution or abundance of species and is omitted from the tables. Other field methods are described elsewhere (Anderson 1970a, 1970b).

Lake locations are reported by Military Grid Reference (Universal Transverse Mercator Grid) taken from 1:50,000-scale maps obtainable from the Canada Department of Energy, Mines and Resources. The lake numbers used in Table 2–8 refer to a master-map system being used by the National and Historic Parks Branch, the letter preceding the number referring to the National Park (N.P.) or other area (i.e. A = montane, Alberta; P = prairie, Alberta and Saskatchewan; BC = montane, British Columbia; B = Banff N.P.; G = Glacier N.P.; J = Jasper N.P.; K = Kootenay N.P.; M = Mt. Revelstoke N.P.; W = Waterton Lakes N.P.; Y = Yoho N.P.).

Identifications and taxonomy generally follow the keys of Dexter, Linder, Mattox, Brooks, Wilson, Yeatman, Wilson and Yeatman, Chace et al. (in Edmondson 1959), supplemented by the keys and data of Brandlova et al. (1972), Goulden (1968), Anderson (1971a), and Hartland-Rowe (1967 and personal communication).

The Study Area

Most of the lakes in this study are located in the mountain National Parks of Alberta and British Columbia. Some are situated in the immediate vicinity of these parks or in the mountains between Banff and Waterton Lakes National Parks. The others are located in the foothills (colline) or prairie (planar) belts of southern Alberta. Figure 1 is a map of the study area.

The lakes in Glacier and Mt. Revelstoke National Parks are in granitic formations, some in Jasper National Park are in feldspathic quartz formations, and most of the remainder of the alpine, subalpine, and montane lakes lie in limestone formations. The foothills lakes are in dark grey or dark grey-wooded soil zones, and the prairie lakes are in thin black or brown soil zones with a saline-soil area extending approximately through the middle of this zone. A brief review of soils and geological formations of the study region can be found in Baird (1963) and Hardy (1967). Except for the lakes in the granitic or feldspathic quartz formations or the saline-soil zone, the chemical analyses of the waters in the study area were remarkably similar, differing mainly in dilution. Ranges of certain features of the 340 lakes and ponds studied are:

Elevation (meters above sea level)	660–2455
Surface area (maximum, in hectares)	<0.1–3940
Depth (maximum known, in meters)	0.5–135.5
Sum of constituents (= TDS[1], ppm)	2–29,800
Maximum heat content (= kcal/liter)	3.8–32
Maximum no. crustacean plankters (per liter)	0–663.5
Total no. crustacean plankton species (per lake)	0–25

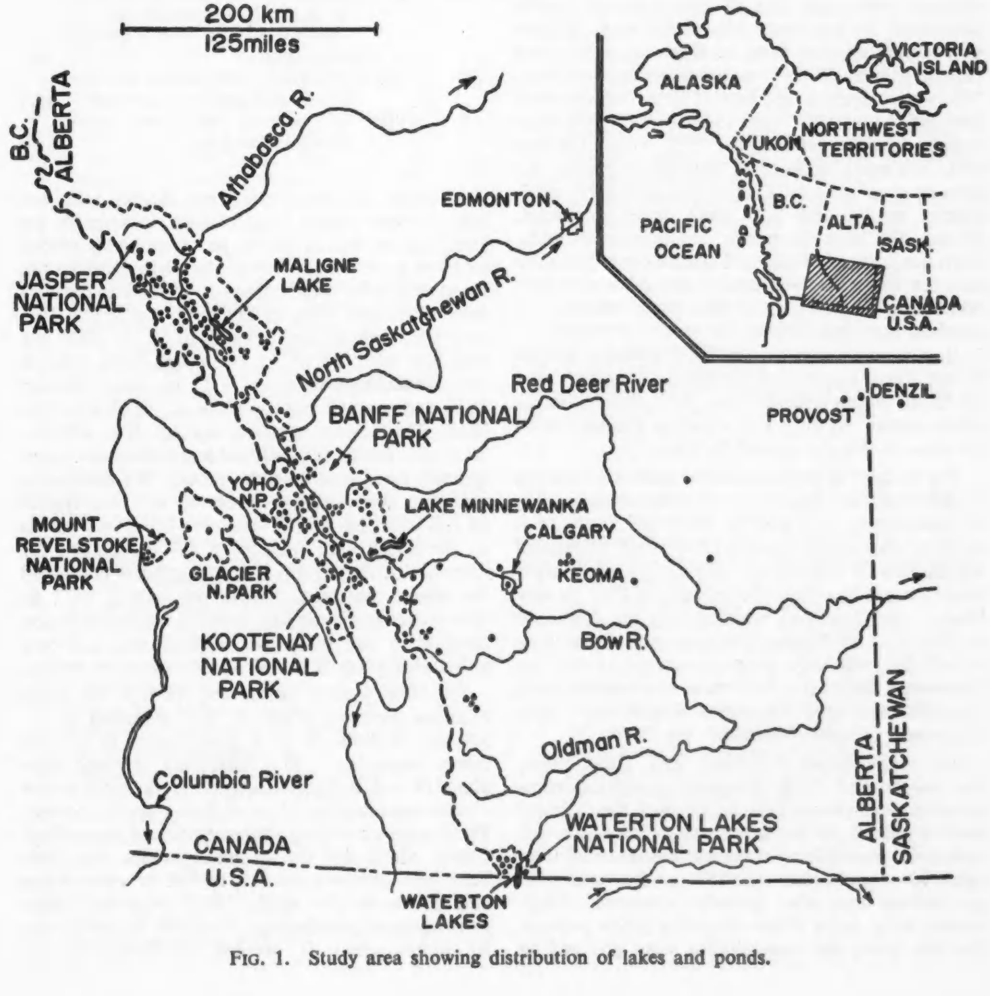

200 km
125miles
B.C.
ALBERTA
Athabasca R.
EDMONTON
JASPER NATIONAL PARK
MALIGNE LAKE
North Saskatchewan R.
ALASKA
VICTORIA ISLAND
YUKON
NORTHWEST TERRITORIES
B.C.
ALTA.
SASK.
PACIFIC OCEAN
CANADA
U.S.A.
Red Deer River
BANFF NATIONAL PARK
PROVOST
DENZIL
YOHO N.P.
LAKE MINNEWANKA
MOUNT REVELSTOKE NATIONAL PARK
GLACIER N.PARK
CALGARY
KEOMA
KOOTENAY NATIONAL PARK
Bow R.
Oldman R.
Columbia River
ALBERTA
SASKATCHEWAN
WATERTON LAKES NATIONAL PARK
CANADA
U.S.A.
WATERTON LAKES

FIG. 1. Study area showing distribution of lakes and ponds.

---

[1] Total dissolved solids.

Of 317 lakes and ponds for which salinity data were available, the mean salinity was 218 ppm. However, by eliminating one (Gooseberry Lake = 29,800 ppm) from the total, the mean for the other 316 waters was only 110 ppm.

Results and Discussion

A total of 97 crustacean species were identified from the 340 lakes and ponds (Table 1) for a total of 1787 species occurrences or populations. Of these, 27% were by only three species: *Acanthocyclops vernalis*, *Chydorus sphaericus*, and *Diaptomus arcticus*. The first two occurred in more than 50% of the 340 waters. Twenty-five of the 97 species occurred only once. The 48 least common species accounted for less than 6% of the total number of occurrences, and none of these occurred more than five times. Of the total number of populations, 798 were copepod species, 51% of which were cyclopoids and 47% were calanoids. Of 904 cladoceran species populations, 28% were *Daphnia* spp. The mean number of crustacean species per lake or pond was 5.27, of which 2.66 were cladoceran species and 2.35 were copepod species. In the 271 lakes or ponds containing calanoids, the mean number of calanoid species per community was 1.4 (range = 1–5), and in 204 lakes or ponds containing *Daphnia* spp., the mean number of *Daphnia* spp. per community was 1.3 (range = 1–3). The maximum number of crustacean species in any one lake or pond plankton community was 25. Small waters generally had more species, somewhat contrary to the observations of Pennak (1957) on some Colorado mountain lakes.

The concept of numerical dominance of a species in the crustacean plankton community (i.e. > 10% of abundance) will not be employed here. Is it unlikely that most species have much ecological significance in the aquatic community when their abundance is less than one animal per liter (density levels 1 and 2, above), whether they are dominant in the sense of Patalas (1971) or not. Exceptions would be relatively large crustaceans such as *Gammarus lacustris*, Anostraca, Notostraca and Conchostraca spp., *Leptodora kindtii*, and large *Diaptomus* (*Hesperodiaptomus*) spp.

For purposes of discussion and presentation, the waters and their crustacean plankton communities were grouped on the basis of the calanoid species present in the lakes and ponds. Although cyclopoid populations occurred more often than calanoid populations (409:371), the cyclopoid populations were often sparsely represented. Diaptomids were more often abundant when present. On this basis, the communities were grouped as follows (number of lakes and ponds supporting each community type is given in parentheses):

Table	Group		
2	I	one or both *Diaptomus shoshone* and *D. arapahoensis*, ± *Leptodiaptomus* spp.	(37)
3	IIA:	*D. arcticus* the only copepod	(55)
4	IIB:	*D. arcticus* + *Leptodiaptomus* spp. ± cyclopoids	(24)
	IIC:	*D. arcticus* + cyclopoid spp.	(24)
	III:	prairie *D. arcticus* or other *Hesperodiaptomus* spp.	(10)
5	IV:	*Acanthodiaptomus denticornis*, *D. leptopus*, *D. forbesi*	(57)
6	V:	*D. tyrrelli*, *D. ashlandi*, *D. sicilis*, *D. nudus*, *D. oregonensis*, *D. franciscanus* or *D. connexus* the only diaptomid	(62)
7	VI:	cyclopoids only, except two very sparse diaptomid occurrences	(53)
8	VII:	no copepods except very sparse cyclopoid nauplii	(18)

Although the elevations, areas, depths, salinities, heat content values, total number of animals per liter, and number of species per community tended to have wide ranges for the lakes in each group, mean values for these parameters for certain groups were of interest. The waters in Group I, IIB, IIC, and VII were at high elevations ($\bar{x} > 2000$ m), had low salinities ($\bar{x} < 100$ ppm), were cold ($\bar{x} < 10$ kcal/liter), deep ($\bar{x} > 13$ m, except Group VII), and sparsely populated ($\bar{x} < 26$ crustaceans/liter). The largest of these, Group IIA, includes lakes and ponds generally colder, higher, and more sparsely populated than the others. The crustacean plankton communities of Group IIA are typical of fish-free alpine and subalpine lakes and ponds in the study area (Anderson 1971b). Except for Group VII, the Group IIA communities contained the fewest crustacean species per lake ($\bar{x} = 2.4$). The waters in Group IIA and VII tended to be the smallest in the study ($\bar{x}$'s = 14.5 and 1.5 ha), although Group IIA had a wide range of values.

The few waters containing Group III communities were at relatively low elevation ($\bar{x} = 970$ m), shallow ($\bar{x} = 1.2$ m), saline ($\bar{x} = 944$ ppm), warm ($\bar{x} = 25.6$ kcal/liter), densely populated ($\bar{x} = 170.5$ crustaceans/liter) lakes with rather diverse communities ($\bar{x} = 9.3$ crustacean species). These waters are fairly representative of the shallow waters which dot the western prairies, but their high heat contents are not typical of other lakes and ponds in this study which supported *Hesperodiaptomus* populations. However, in the Group III waters where *D. arcticus*, *D. breweri*, or *D.*

novemdecimus occurred, these large copepods developed quickly during the spring period and disappeared for the remainder of the ice-free season.

Waters containing Group IV communities tended to be mostly montane ($\bar{x}$ = 1328 m), small ($\bar{x}$ = 15.2 hectare) and densely populated ($\bar{x}$ = 105 crustaceans/liter) lakes and ponds having rather diverse ($\bar{x}$ = 9.4 spp.) crustacean communities. Except for the *D. forbesi* lakes, considered below, Group IV communities generally occurred in

TABLE 1. List of species in the crustacean plankton communities for the 340 lakes and ponds. The number of communities in which each species was found in shown to the left.

2	*Senecella calanoides* Juday 1923
13	*Acanthodiaptomus denticornis* (Wierzejski) 1888
16	*Diaptomus arapahoensis* Dodds 1915
23	*Diaptomus shoshone* S. A. Forbes 1893
1	*Diaptomus novemdecimus* M.S. Wilson 1953
1	*Diaptomus hirsutus* M.S. Wilson 1953
5	*Diaptomus nevadensis* Light 1938
124	*Diaptomus arcticus* Marsh 1920
1	*Diaptomus breweri* M.S. Wilson 1958
1	*Diaptomus franciscanus* Lilljeborg 1889
1	*Diaptomus victoriaensis* Reed 1958
46	*Diaptomus leptopus* S.S. Forbes 1882
7	*Diaptomus forbesi* Light 1938
68	*Diaptomus tyrrelli* Poppe 1888
26	*Diaptomus sicilis* S.A. Forbes 1882
1	*Diaptomus connexus* Light 1938
3	*Diaptomus ashlandi* Marsh 1893
27	*Diaptomus nudus* Marsh 1904
1	*Diaptomus assiniboiaensis* Anderson 1971
3	*Diaptomus sanguineus* S.A. Forbes 1876
1	*Diaptomus oregonensis* Lilljeborg 1889
14	*Orthocyclops modestus* (Herrick) 1883
1	*Macrocyclops ater* (Herrick) 1882
43	*Macrocyclops albidus* (Jurine) 1820
55	*Eucyclops agilis* (Koch) 1838
9	*Eucyclops speratus* (Lilljeborg) 1901
179	*Acanthocyclops vernalis* Fischer 1853
7	*Diacyclops navus* Herrick 1882
93	*Diacyclops bicuspidatus thomasi* S.A. Forbes 1882
8	*Microcyclops varicans rubellus* Lilljeborg 1901
14	*Canthocamptus oregonensis* M.S. Wilson 1956
4	*Bryocamptus zschokkei* (Schmeil) 1893
4	*Leptodora kindtii* (Focke) 1844
49	*Polyphemus pediculus* (Linné) 1761
7	*Sida crystallina* (O.F. Müller) 1776
1	*Latona setifera* (O.F. Müller) 1785
12	*Diaphanosoma brachyurum* (Liéven) 1848
12	*Diaphanosoma leuchtenbergianum* Fischer 1850
20	*Holopedium gibberum* Zaddach 1855
13	*Eurycercus lamellatus* (O.F. Müller) 1785
9	*Acroperus harpae* Baird 1843
6	*Graptoleberis testudinaria* (Fischer) 1848
2	*Leydigia quadrangularis* (Leydig) 1860
1	*Alona quadrangularis* (O. F. Müller) 1785
37	*Alona guttata* Sars 1862
16	*Alona affinis* (Leydig) 1860
5	*Alona costata* Sars 1862
13	*Alona rectangula* Sars 1861
5	*Alona intermedia* Sars 1862
22	*Alonella nana* (Baird) 1850
7	*Alonella excisa* (Fischer) 1854
1	*Alonella exigua* (Lilljeborg) 1853
174	*Chydorus sphaericus* (O.F. Müller) 1785
3	*Chydorus ovalis* Kurz 1874
1	*Pleuroxus striatus* Schoedler 1863
3	*Pleuroxus procurvus* Birge 1878
1	*Pleuroxus aduncus* (Jurine) 1820
3	*Pleuroxus denticulatus* Birge 1878
1	*Pleuroxus trigonellus* (O.F. Müller) 1785
2	*Daphnia magna* Straus 1820
4	*Daphnia similis* Claus 1876
1	*Daphnia longiremis* Sars 1861
52	*Daphnia rosea* Sars 1862 emend. Richard 1896
19	*Daphnia galeata* Sars 1864 *mendotae* Birge 1913
55	*Daphnia middendorffiana* Fischer 1851
61	*Daphnia pulex* Leydig 1860 emend. Richard 1896
19	*Daphnia pulicaria* Forbes 1893 emend. Hrbáček 1959
37	*Daphnia schoedleri* Sars 1862
10	*Daphnia catawba* Coker 1926
1	*Daphnia parvula* Fordyce 1901
28	*Simocephalus vetulus* Schoedler 1858
1	*Simocephalus serrulatus* (Koch) 1841
26	*Scapholeberis kingi* Sars 1903
26	*Ceriodaphnia affinis* Lilljeborg 1900
16	*Ceriodaphnia reticulata* (Jurine) 1820
2	*Ceriodaphnia acanthina* Ross 1897
8	*Ceriodaphnia lacustris* Birge 1893
5	*Ceriodaphnia pulchella* Sars 1862
21	*Ceriodaphnia quadrangula* (O.F. Müller) 1785
1	*Moina macrocopa* (Straus) 1820
80	*Bosmina longirostris* (O.F. Müller) 1785
1	*Macrothrix hirsuticornis* Norman and Brady 1867
3	*Branchinecta gigas* Lynch 1937
4	*Branchinecta mackini* Dexter 1956
1	*Branchinecta campestris* Lynch 1960
1	*Branchinecta lindahli* Packard 1883
18	*Branchinecta paludosa* (O.F. Müller) 1788
1	*Eubranchipus bundyi* (Forbes) 1876
4	*Eubranchipus intricatus* Hartland-Rowe 1967
3	*Streptocephalus seali* Ryder 1879
1	*Artemiopsis stephanssoni* Johansen 1922
5	*Lynceus brachyurus* O.F. Müller 1785
2	*Lepidurus lynchi* Linder 1952
2	*Lepidurus apus* (Linné) 1758
27	*Gammarus lacustris lacustris* Sars 1865
12	*Hyallella azteca* (Saussure) 1858
1	*Mysis relicta* Lovén 1861

TABLE 2. Crustacean plankton density, species composition and abundance,

Lake no.	Name	Grid reference	Sampling date, chemistry	Elevation (*m*)	Area (*ha*)	Max known depth (*m*)	Secchi max (*m*)	*p*H	TDS[c] (*ppm*)	Max heat content (*kcal*)	No./liter max
J 14	Nigel L.	11U/MJ863886	19.6.70	2400	32.0	7.0	0.7	8.0	67	7.1	21.3
J 774	Up. Trapper L.	11U/MJ534332	8.9.67	2090	4.0	11.5	7.0	7.4	6	8.0[b]	4.3
J 775	Up. Trapper P.	11U/MJ543349	11.9.68	2300	0.7	7.0	2.5	7.7	9[e]	10.0[b]	2.8
J 453	O'Beirne #1	11U/LJ922647	19.8.70	2133	4.7	24.0	8.5	7.4	8[e]	7.6	2.9
J 448	O'Beirne #2	11U/LJ923626	19.8.70	2027	8.5	33.0	12.5	7.4	7	7.3	1.4
J 452	O'Beirne #5	11U/LJ922617	19.8.70	2000	6.4	33.0	11.0	7.7	12	7.4	2.9
J 441	Outer Rink L.	11U/LJ936646	19.8.70	2027	9.5	18.0	12.5	7.6	38	8.0	5.4
J 310	Moat L.	11U/MJ105420	19.8.70	1945	50.0	11.0	8.5	7.5	34	11.4	11.4
J 308	Amethyst L.	11U/MJ140378	19.8.70	1967	470.0	21.0	11.5	7.4	26	10.1	4.4
J 191	Beryl L.	11U/MJ235335	19.8.70	2043	22.0	31.0	2.0	7.5	53	6.7	1.0
J 178	Whirlpool L.	11U/MJ356224	28.8.69	2087	12.0	29.0	2.0	7.4	18	7.0	0.6
J *50*	*Catacombs L.*	*11U/MJ470092*	*28.8.69*	*2058*	*9.0*	*15.0*	*6.0*	*7.5*	43	–	2.5
J 217	Lo. Trapper L.	11U/MJ536329	8.9.67	2087	7.0	19.0	5.5	7.4	6	8.0[b]	1.0
J 139	Replica P.	11U/MJ692175	7.9.67	2228	2.5	7.0	5.0	7.2	15	12.0[b]	1.0
J 90	Lazuline L.	11U/MJ829158	7.9.67	2255	2.0	11.0	1.8	8.1	80	10.5	1.8
J 132	Oreamnos L.	11U/MJ853186	7.9.67	2300	9.0	12.0	2.5	7.9	81	8.4	0.2
J 74	Phalarope L.	11U/MJ704153	7.9.67	2220	1.5	6.0	5.0	7.0	5	8.0[b]	1.6
J *76*	*Branchinecta P.*	*11U/MJ709148*	*7.9.67*	2270	0.5	2.5	3.5	7.0	5	9.0[b]	0.2
J *358*	Surprise #1	*11U/MJ580495*	*16.7.70*	*1661*	*25.0*	*6.2*	*2.4*	*8.3*	*127*	14.4	*19.0*
A	Teardrop P.	11U/PF823630	12.8.69	2030	0.4	1.5	1.0	9.8	41	18.2	75.0
A	Plateau P.	11U/PF778671	11.8.66	2180	0.5	5.0	1.0	7.8	86	17.0	100.0
A	Rae Tarn	11U/PG434133	22.8.66	2180	3.3	3.5	+[d]	8.7	117	9.1	85.2
A	Elbow L.	11U/PG412116	22.8.66	2140	8.0	8.0	7.0	7.9	188	9.4	56.9
A	Picklejar #2	11U/PF577986	9.10.69	2165	2.3	6.4	–	8.1	119	–	35.1
A	Lawson L.	11U/PG206164	5.9.69	2206	13.0	6.1	–	8.2	86	–	12.6
A	Up. Galatea L.	11U/PG215357	2.9.69	2225	6.0	10.0	–	7.9	50	–	3.0
A	*Lo. Galatea L.*	*11U/PG222362*	*2.9.69*	*2193*	*7.0*	*18.6*	–	*8.0*	*60*	–	*5.2*
W 4	Lineham hourglass	11U/QE148396	15.8.71	2111	12.0	22.6	11.5	8.1	42	5.9	1.4
W 1	N. Lineham L.	11U/QE138400	15.8.71	2170	20.0	28.7	9.5	8.1	42	9.2	1.3
W 5	Mid. Rowe L.	11U/QE152373	26.7.71	2162	1.4	6.0	+[d]	8.1	14	13.9	46.0
W 3	Up. Rowe L.	11U/QE149371	21.7.70	2168	6.5	2.5	+[d]	7.8	13	13.1	62.7
W 55	Lost L.	11U/QE083475	8.8.67	1875	2.0	10.5	7.5	7.6	41	6.9	187.7
W 6	Lo. Rowe L.	11U/QE156374	21.6.71	1957	2.0	7.0	+[d]	7.8	30	10.2	26.6
W 2	S. Lineham L.	11U/QE138394	14.8.71	2165	5.0	17.0	9.5	8.1	37	8.7	8.0
W 7	Cameron L.	11U/QE160330	22.7.70	1660	150.0	34.0	19.5	7.8	44	10.2	20.0
W 8	Little Cameron	11U/QE164341	3.9.71	1655	4.0	5.0	+[d]	7.4	32	11.3	8.1
W 58	Lo. Twin L.	11U/QE078458	22.7.70	1927	3.0	8.0	7.5	7.6	52	12.5	89.1

[a] Blanks indicate no data.
[b] Estimates from incomplete data.
[c] Ca > Mg and HCO: > SO: in all lakes except those where $SO_4 > HCO_3$.
[d] + indicates clearly visible on bottom.
[e] ? slight uncertainty in identification.

moderately deep, low salinity lakes accumulating only a moderate amount of heat at peak temperatures. Group V communities occurred in lakes lacking much uniformity and are considered by species below.

Group VI communities inhabited a scattered group of lakes and ponds diverse in certain respects, but rather uniform in others. Almost all these waters contained either substantial populations of fish or *Chaoborus* spp. In general, they were high elevation ($\bar{x}$ = 1843 m), large ($\bar{x}$ = 39.8 hectare), deep ($\bar{x}$ = 12.9 m), low salinity ($\bar{x}$ = 67.1 ppm) waters with simple crustacean communities ($\bar{x}$ = 3.6 crustacean spp.). The range for the maximum heat accumulation for this group was rather wide, although none exceeded 19.1 kcal/liter and the mean for the group was only 11.2 kcal/liter.

In general, in the lakes of this study crustacean plankton density and species diversity tended to be greater at higher salinities (see also Patalas 1964), the main exceptions being the highly saline prairie lakes which had fewer species than more dilute lakes and ponds in their immediate vicinity. Of the 340 waters of the present study, however, the lake with the highest plankton density (Indian Springs = 663.5 crustaceans/liter; TDS = 206 ppm) and the one showing the greatest diversity (Maskinonge = 25 spp.; TDS = 204 ppm) were not highly saline. It is likely that abundance may be more closely linked to heat accumulation, and that diversity and some limnological features for 37 Group I lakes and ponds.•

Crustacean community			*Holopedium gibberum*	*Alona guttata*	*Alona rectangula*	*Chydorus sphaericus*	*Daphnia rosea*	*Daphnia galeata mendotae*	*Daphnia middendorffiana*	*Daphnia pulex*	*Daphnia schoedleri*	*Simocephalus vetulus*	*Ceriodaphnia affinis*	*Ceriodaphnia reticulata*	*Ceriodaphnia quadrangula*	*Bosmina longirostris*	*Diaptomus arapahoensis*	*Diaptomus shoshone*	*Diaptomus arcticus*	*Diaptomus victoriaensis*	*Diaptomus tyrrelli*	*Diaptomus ashlandi*	*Macrocyclops albidus*	*Eucyclops agilis*	*Acanthocyclops vernalis*	*Diacyclops bicuspidatus thomasi*	*Canthocamptus oregonensis*	*Bryocamptus zschokkei*	*Branchinecta paludosa*	*Eubranchipus intricatus*	*Gammarus lacustris*	*Hyalella azteca*
Total no. spp	Cladocera spp	Copepoda spp																														
3	1	2	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	4	.	.	.	.	.	.	2	.	.	.	.	.	.	.
6	4	2	3	1	.	1	.	.	2	.	.	.	.	.	.	.	.	2	.	.	.	.	.	.	.	3	.	.	.	.	.	.
6	3	2	3	.	.	1	.	.	2	.	.	.	.	.	.	.	.	2	.	.	.	.	.	.	1?•	.	.	.	1	.	.	.
3	1	2	.	.	.	.	.	.	3	.	.	.	.	.	.	.	.	2	.	.	.	.	.	.	3	.	.	.	.	.	.	.
6	2	3	3	.	.	.	.	.	2	.	.	.	.	.	.	.	.	1	2	.	.	.	.	.	2	.	.	.	1	.	.	.
5	2	2	3	.	.	.	.	.	2	.	.	.	.	.	.	.	.	1	2	.	.	.	.	.	.	.	.	.	1	.	.	.
5	1	3	.	.	.	.	.	.	3	.	.	.	.	.	.	.	.	1	3	.	.	.	.	.	.	2	.	.	.	.	1	.
4	0	4	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	2	.	3	.	.	.	3	.	.	.	.	.	.	.
7	3	4	2	1	.	.	.	.	2	.	.	.	.	.	.	.	.	1	3	.	3	.	.	.	2	.	.	.	.	.	.	.
4	1	3	.	.	.	.	.	.	2	.	.	.	.	.	.	.	.	1	2	.	.	.	.	.	.	1	.	.	.	.	.	.
4	2	2	.	.	.	1	.	.	1	.	.	.	.	.	.	.	.	1	2	.	.	.	.	.	.	.	.	.	.	.	.	.
5	2	3	.	.	.	2	.	.	2	.	.	.	.	.	.	.	.	1	2	.	.	.	.	.	1?•	.	.	.	.	.	.	.
4	1	3	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	1	2	.	.	.	.	.	.	2?•	.	.	.	.	.	.
5	2	3	.	1	.	.	.	.	1	.	.	.	.	.	.	.	.	1	2	.	3	.	.	.	.	.	.	.	.	.	.	.
6	2	4	.	1	.	1	.	.	.	.	.	.	.	.	.	.	.	1	2	.	3	.	.	.	1?•	.	.	.	.	.	.	.
5	2	3	.	.	.	1	.	.	1	.	.	.	.	.	.	.	.	1	1	.	.	.	.	.	.	.	.	1?•	.	.	.	.
3	0	2	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	2	.	.	3	.	.	.	.	.	.	.	.	.	1	.
4	1	2	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.	1	.	.	1	.	.	.	.	.	.	.	1	.	.	.
5	1	3	.	.	.	.	.	.	2	.	.	.	.	.	.	.	.	2	.	.	.	4	.	.	2?•	.	.	.	1	.	.	.
9	4	4	.	.	1	3	.	.	.	1	.	1	.	.	.	.	.	3	.	.	4	.	.	.	.	1?•	1	.	.	2	.	.
5	1	3	.	.	.	.	.	.	.	2	.	.	.	.	.	.	.	2	.	4	.	.	.	.	1	.	.	.	2	.	.	.
10	3	6	.	1	.	2	.	.	.	.	4	.	.	.	.	.	2	.	.	.	.	.	1	1	1	4	1	.	.	.	1	.
4	2	2	.	.	.	2	.	.	.	.	2	.	.	.	.	.	4	.	.	.	.	.	.	.	2	.	.	.	.	.	.	.
5	1	3	.	.	.	.	.	2	.	.	.	.	.	.	.	.	2	.	.	.	.	.	1	.	.	4	.	.	.	.	1	.
4	1	3	.	.	.	.	.	.	.	3	.	.	.	.	.	.	4	.	1	.	.	.	.	.	1	.	.	.	.	.	.	.
3	0	2	.	.	.	.	.	.	.	.	.	.	.	.	.	.	3	.	2	.	.	.	.	.	.	.	.	.	1	.	.	.
5	3	2	.	.	.	1	.	.	3	.	.	.	.	.	.	1	3	.	3	.	.	.	.	.	.	.	.	.	.	.	.	.
3	0	3	.	.	.	.	.	.	.	.	.	.	.	.	.	.	2	.	3	.	.	.	.	.	1?•	.	.	.	.	.	.	.
3	0	3	.	.	.	.	.	.	.	.	.	.	.	.	.	.	2	.	3	.	.	.	.	.	1	.	.	.	.	.	.	.
6	3	3	4	.	.	1	.	.	3	.	.	.	.	.	.	.	4	2	.	.	.	.	.	.	1	.	.	.	.	.	.	.
5	2	3	.	.	.	1	.	.	1	.	.	.	.	.	.	.	4	1	.	.	.	.	.	1	.	.	.	.	.	.	.	.
8	4	3	.	.	.	.	3	.	1	.	.	.	.	1?•	1	.	3	.	.	.	.	.	.	.	.	4	1	.	1	.	.	.
4	2	2	.	.	.	.	.	1	.	.	.	.	.	.	.	3	4	.	.	.	.	.	.	.	3?•	.	.	.	.	.	.	.
2	0	2	.	.	.	.	.	.	.	.	.	.	.	.	.	.	3	.	.	.	.	.	.	.	2	.	.	.	.	.	.	.
5	3	2	.	.	.	.	3	.	.	.	2	.	.	.	.	1	3	.	.	.	.	.	.	.	3	.	.	.	.	.	.	.
9	4	4	.	.	.	1	.	.	.	2?•	.	.	1	.	.	3	1	.	.	.	.	.	.	1	1	.	.	1	.	.	.	1
8	5	3	2	.	.	.	1	1?•	.	.	.	.	2	.	.	1	4	.	.	.	.	.	.	1	.	4	.	.	.	.	.	.

is related to wide seasonal fluctuations in certain parameters such as heat, salinity, and depth.

Although diel vertical migrations for copepods have not been examined in any of the lakes of my study, certain other crustacean species not usually considered part of the zooplankton may occupy important ecological niches in the plankton communities during part of the day. For example, *Mysis relicta* migrates upward at night and may remain in the water column during dull weather, and what appears to be a nocturnal migration by *Gammarus lacustris* into the limnetic zone of some lakes containing fish may in fact represent normal diel behavior by *G. lacustris*, such adventurers being eaten as they enter the limnetic zone during daylight hours. Observations and other studies (in preparation) indicate that *G. lacustris* may be planktonic much of the time in certain fish-free lakes. *G. lacustris* occurred limnetically more frequently in winter in some lakes (e.g. Linnet Lake) but was not seen to be active in winter in others (e.g. Thurston's Pond T-2). Lötmarker (1964) suggested that samples collected during daylight hours may not be representative of the plankton communities, at least in some lakes. However, he did not sample the bottom or the inshore regions of the lakes in his study, and he assumed that nocturnal vertical migration would compensate for the absence of samples from the bottom 10 m. Most samples in my study were

TABLE 3. Crustacean plankton density, species composition and abundance,

Lake no.	Name	Grid reference	Date for chem data	Elevation (m)	Area (ha)	Max known depth (m)	Secchi depth (m) max known	pH	TDS (ppm)
J 564	Moraine P.	11U/MJ917886	12.9.68	2072	1.0	5.0	3.0	7.9	18
J 522	Porcupine L	11U/MJ011761	12.9.68	2040	19.0	27.5	15.0	8.0	58
J 482	N. Kerr L	11U/MJ169660	12.9.68	2140	5.0	11.3	4.5	7.6	5[e]
J 483	S. Kerr L	11U/MJ170657	12.9.68	2180	1.4	7.0	3.0	7.5	4[e]
J 484	Kerr P.	11U/MJ173662	12.9.68	2172	1.0	3.0	+[d]	7.5	4[e]
J 487	N. Cairngorm L.	11U/MJ185657	12.9.68	2370	5.0	10.0	7.5	8.1	2
J 778	Up. Cavell L	11U/MJ313369	9.7.66	2317	2.0	6.2	4.5	8.0	33
J 183	Beacon L.	11U/MJ140215	28.8.69	2145	80.0	46.0	5.0	7.7	3
J 172	Divergence L.	11U/MJ342170	28.8.69	1875	55.0	38.0	2.0	8.0	9
J 39	Lick L.	11U/MJ404103	28.8.69	1967	7.5	18.0	5.0	7.7	2
J 801	Lick Pk. P.	11U/MJ378140	28.8.69	2320	0.2	6.0	6.0	7.4	3
J 284	Lo. Antler L.	11U/MJ452448	11.9.68	2125	1.0	8.0	6.0	7.9	29
J 283	Caribou L.	11U/MJ462434	11.9.68	2200	2.5	9.0	5.0	7.9	30
J 345	Amber #1	11U/MJ404518	11.9.68	2292	1.0	7.0	2.0	8.0	66
J 345A	Amber #2	11U/MJ402518	11.9.68	2287	1.0	6.7	3.0	8.0	66
J 346	Amber #3	11U/MJ401517	11.9.68	2226	0.2	5.0	3.5	8.0	66
J 346A	Amber #4	11U/MJ401515	11.9.68	2225	1.0	8.5	3.5	8.0	66
J 220	Ultramaligne	11U/MJ666275	8.9.67	2287	20.0	30.0	0.7	8.3	55
J 72	S. Pika L.	11U/MJ698152	7.9.67	2245	3.0	10.0	1.2	6.6	5
J 71	N. Pika L	11U/MJ697154	7.9.67	2245	3.0	9.0	1.6	6.6	5
J 141	Up. Ouzel L.	11U/MJ677177	7.9.67	2310	3.0	6.0	2.0	7.1	18
J 223	Up. Southesk	11U/MJ777297	20.8.70	2325	26.0	26.0	0.5	8.3	83
J 264	Rocky #1	11U/MJ694393	20.8.70	2094	4.0	5.0	4.1	8.2	115
J 259	Wolf	11U/MJ735372	20.8.70	2127	90.0	49.0	2.0	8.2	91
B 290	Up. Dolomite P.	11U/NH427269	29.8.67	2385	1.0	3.0	3.0	8.5	9
B 288	Katherine L.	11U/NH421260	29.7.66	2370	11.0	11.0	6.0	7.9	71
B 272	Turquoise L.	11U/NH423135	8.66	2149	21.0	–	–	–	–
B 89	Moraine L.	11U/NG570858	20.9.67	1887	42.0	20.5	8.5	7.5	65
B 68	Sentinel L.	11U/NG543871	12.9.67	2424	2.4	6.7	6.7	7.9	61
B 87	Eiffel L.	11U/NG528856	7.8.66	2249	7.8	13.5	+[d]	7.5	38
B 171	Annette L.	11U/NG552907	28.8.68	1965	4.8	13.0	–	8.4	–
B 49	Black Rock L.	11U/NG760636	25.8.68	2200	5.7	23.0	–	7.2	–
B 230	Lost Horse L.	11U/NH927042	1.8.68	2323	4.0	7.0	4.0	8.4	65
B 229	Crescent L.	11U/NH928057	1.8.68	2204	4.0	5.5	–	8.5	128
B 500	Little Bighorn L.	11U/NH937001	23.9.67	2420	0.8	8.0	5.0	8.1	163
B 142	Goat L.	11U/NG794999	20.7.66	2438	–	–	–	8.2	75
B 124	Cascade L.	11U/NG978809	23.9.67	2332	7.7	10.0	3.5	7.9	87
B 10	Owl L.	11U/PG033353	9.7.70	1881	34.0	23.5	–	8.3	96
Y 50	Fairy L.	11U/NH363107	9.9.69	2232	12.0	21.0	7.0	8.5	149[e]
Y 37	Kiwetinok L.	11U/NH278073	9.9.69	2455	6.0	15.0	5.0	8.3	53
Y 55	Amiskwi L.	11U/NH247155	9.9.69	2088	6.0	9.8	2.5	8.3	176
Y 61	Indigo L.	11U/NH204109	9.9.69	2272	4.0	43.0	14.0	8.3	72
Y 35	Otto L.	11U/NH198023	9.9.69	2060	0.7	6.4	+[d]	8.4	62
Y 29	Crystal L.	11U/NG206974	9.9.69	2206	1.2	2.0	+[d]	8.1	64
Y 38	Hamilton L.	11U/NH294004	9.9.69	2140	5.0	12.2	10	8.3	71
Y 16	Oesa L.	11U/NG486893	5.8.66	2285	16.2	39.0	6.0	7.8	53
Y 14	Opabin #2	11U/NG475880	31.7.68	2233	1.8	3.5	+[d]	8.2	9
Y 15	Opabin #1	11U/NG481877	20.9.67	2270	3.2	12.3	2.8	8.3	33
K 25	Floe L.	11U/NG613558	12.9.70	2027	54.0	16.0	2.0	–	–
G 8	Fidelity L.	11U/MG506766	30.6.70	1866	3.0	5.0	+[d]	7.4	42
W 24	Crypt L.	12U/TK923313	12.8.71	1963	14.0	44.2	9.0	8.1	25
A	Ribbon L.	11U/PG236384	31.8.69	2070	4.0	16.2	–	8.2	125
A	Pinto L.	11U/NH094747	21.8.69	1759	115.0	30.5	10.7	–	–
A	Landslide	11U/NH307700	11.8.72	1982	50.0	18.3	–	7.5	66
A	Burstall #1	11U/PG180270	27.8.66	1957	8.0	7.5	0.5	8.1	120

[a]Footnotes as in Table 2

collected during daylight hours, but precautions were taken to ensure that vertical tows were begun at or within a few centimeters of the bottom of the lake. Observations and supplementary sampling at night, near bottom, and in inshore regions indicated that almost all species present were represented in the plankton samples.

The values of such observations and supplementary samplings were frequently obvious in this study. Diaptomid copepods were often observed at the water's surface on extremely bright days, especially *Hesperodiaptomus* spp. in alpine lakes. What sometimes seemed to be swarms of copepods at the surface or near shore may have been aggregations and some limnological features for 55 Group IIA lakes and ponds.[a]

	Crustacean plankton																		
Heat content (*kcal*)[b]	Max no./ liter	Total no. spp	Cladocera spp	Copepoda spp	*Alona guttata*	*Alona costata*	*Chydorus sphaericus*	*Daphnia middendorffiana*	*Daphnia pulex*	*Daphnia pulicaria*	*Bosmina longirostris*	*Diaptomus arcticus*	*Eucyclops agilis*	*Eucyclops speratus*	*Diacyclops bicuspidatus thomasi*	*Acanthocyclops vernalis*	*Branchinecta paludosa*	*Artemiopsis stephanssoni*	*Gammarus lacustris*
5.6	0.2	3	1	2	.	.	.	1	.	.	.	2	.	.	.	1	.	.	.
–	0.7	1	0	1	.	.	.	.	.	.	.	2	.	.	.	.	.	.	.
–	2.3	3	1	2	.	.	1	.	.	.	.	3	.	.	1?[c]	.	.	.	.
–	0.6	3	1	2	.	.	2	.	.	.	.	2	.	.	1?[c]	.	.	.	.
–	3.9	3	1	2	.	.	1	.	.	.	.	3	.	.	1	.	.	.	.
–	3.4	1	0	1	.	.	.	.	.	.	.	3	.	.	.	.	.	.	.
–	7.2	3	1	2	.	.	.	2	.	.	.	3	.	.	1	.	.	.	.
6.3	3.0	2	1	1	.	.	.	2	.	.	.	3	.	.	.	.	.	.	.
6.8	1.9	2	1	1	.	.	.	2	.	.	.	3	.	.	.	.	.	.	.
–	10.0	2	1	1	.	.	.	1	.	.	.	3	.	.	.	.	.	.	.
–	0.3	3	2	1	.	.	1	2	.	.	.	2	.	.	.	.	.	.	.
–	2.0	1	0	1	.	.	.	.	.	.	.	3	.	.	.	.	.	.	.
–	3.9	2	1	1	.	.	.	2	.	.	.	3	.	.	.	.	.	.	.
–	1.0	3	1	2	.	.	1	.	.	.	.	2	.	.	.	1?[c]	.	.	.
–	0.7	3	1	2	.	.	1	.	.	.	.	2	.	.	.	1?[c]	.	.	.
–	0.3	1	0	1	.	.	.	.	.	.	.	2	.	.	.	.	.	.	.
–	0.3	1	0	1	.	.	.	.	.	.	.	2	.	.	.	.	.	.	.
5.3	0.4	1	0	1	.	.	.	.	.	.	.	2	.	.	.	.	.	.	.
9.5	0.1	2	1	1	.	.	1	.	.	.	.	1	.	.	.	.	.	.	.
9.5	0.1	3	2	1	.	.	1	1	.	.	.	1	.	.	.	.	.	.	.
8.9	0.3	1	0	1	.	.	.	.	.	.	.	2	.	.	.	.	.	.	.
4.7	0.6	2	0	2	.	.	.	.	.	.	.	2	.	.	.	1	.	.	.
9.1	4.7	3	2	1	.	.	1	.	2	.	.	3	.	.	.	.	.	.	.
7.7	0.8	3	1	2	.	.	.	.	2	.	.	2	.	.	.	1	.	.	.
14.2	1.0	4	1	2	.	2	.	.	.	.	.	2	.	.	.	1	.	2	.
6.2	1.0	1	0	1	.	.	.	.	.	.	.	2	.	.	.	.	.	.	.
–	2.0	1	0	1	.	.	.	.	.	.	.	3	.	.	.	.	.	.	.
7.7	0.2	3	1	2	.	.	1	.	.	.	.	2	.	.	.	1	.	.	.
7.3	2.9	2	1	1	.	.	.	3	.	.	.	3	.	.	.	.	.	.	.
7.4	2.8	2	1	1	.	.	.	1	.	.	.	3	.	.	.	.	.	.	.
9.0	18.8	1	0	1	.	.	.	.	.	.	.	4	.	.	.	.	.	.	.
10.0	10.6	3	1	2	.	.	1	.	.	.	.	4	.	.	.	1?[c]	.	.	.
4.5	5.9	5	2	2	.	.	2	3	.	.	.	3	.	.	.	1?[c]	2?[c]	.	.
8.8	8.8	5	2	2	.	.	1	3	.	.	.	3	.	.	.	1?[c]	.	.	1
7.3	8.8	5	2	2	.	.	1	3	.	.	.	3	.	.	1?[c]	.	3	.	.
–	0.1	1	0	1	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.
8.7	2.4	3	2	1	.	.	2	2	.	.	.	3	.	.	.	.	.	.	.
8.0[b]	2.9	3	2	1	.	.	1	2	.	.	.	3	.	.	.	.	.	.	.
7.0	0.7	3	2	1	.	.	1	.	1?[c]	.	.	2	.	.	.	.	.	.	.
7.0	1.2	2	1	1	.	.	1	.	.	.	.	3	.	.	.	.	.	.	.
7.3	2.1	2	1	1	.	.	.	2	.	.	.	3	.	.	.	.	.	.	.
5.6	0.9	1	0	1	.	.	.	.	.	.	.	2	.	.	.	.	.	.	.
6.4	0.6	1	0	1	.	.	.	.	.	.	.	2	.	.	.	.	.	.	.
9.1	7.5	1	0	1	.	.	.	.	.	.	.	3	.	.	.	.	.	.	.
12.2	0.7	3	1	2	1	.	.	.	.	.	.	2	1	.	.	.	.	.	.
5.1	0.1	1	0	1	.	.	.	.	.	.	.	2	.	.	.	.	.	.	.
8.7	4.2	3	2	1	.	.	2	2	.	.	.	3	.	.	.	.	.	.	.
7.5	4.4	2	1	1	.	.	1	.	.	.	.	3	.	.	.	.	.	.	.
8.0[b]	0.2	1	0	1	.	.	.	.	.	.	.	2	.	.	.	.	.	.	.
–	1.2	3	1	2	.	.	1	.	.	.	.	3	.	.	1	.	.	.	.
6.7	2.3	2	0	2	.	.	.	.	.	.	.	3	.	.	.	1	.	.	.
–	11.1	4	2	2	.	.	1	.	.	.	1	4	.	.	.	1	.	.	.
–	8.7	5	3	2	.	.	1	2	.	.	1	3	.	.	.	3	.	.	.
4.0[b]	1.0	6	3	3	.	.	1	.	.	2	1	2	.	2	1	.	.	.	.
9.5[b]	0.1	1	0	1	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.

caused by wind-induced currents. On a few occasions, the limnetic zones of certain small alpine lakes and ponds were almost devoid of the large *Diaptomus* spp. which were usually abundant there (e.g. Little Bighorn, Nigel, Plateau, and Teardrop). At these times, the copepods were concentrated near shore on the rocks or near bottom in shallow water, apparently feeding on "Aufwuchs." Direct observation was possible because of the clear water and the absence of macrophytes. Similar copepod behavior was observed under the ice in winter in some ponds. At times, anostracans also congregated near shore or bottom in certain lakes, apparently feeding in much the same way as copepods. Avoidance of inshore regions was especially apparent in *Daphnia similis*, and appeared to be a feature of most *Daphnia* spp. populations. Although many crustacean genera were more common either littorally or pelagically, none was confined exclusively to either zone. A species collected only in a narrow inshore zone of one lake was sometimes pelagic in another, or in the same lake at another time. That a species can and will move from one zone to the other when competition, predation, or other factors are modified has been noted elsewere (Anderson 1970a; Anderson and Raasveldt 1974).

Among species occurring more abundantly in inshore samples were *Macrocyclops albidus*, harpacticoids, *Scapholeberis kingi*, *Acroperus harpae*, *Polyphemus pediculus*, and *Hyalella azteca*. *Senecella calanoides* was collected only in deep tows in the Waterton Lakes (cf. Patalas 1971; Wilson 1972). In this study, *Orthocyclops modestus* tended to be abundant only near bottom in deep and moderately deep lakes, in contrast to the findings of Patalas. Despite the fact that within the general study area, *M. albidus* tended to be an inshore or shallow-water species and *O. modestus* tended to be a deepwater species, *O. modestus* (14 lakes) and *M. albidus* (43 lakes) occurred together only twice (Group IV) where both were sparsely represented. *Branchinecta paludosa* adults were collected only near bottom from a few deep lakes, but it is not known whether the species completes its life cycle in the lakes. In some alpine lakes having no true littoral zone and containing fish, *G. lacustris* and sometimes *Diaptomus arcticus* occurred sparsely only near bottom in deep water.

In general, abundance in winter plankton communities was lower and there were fewer species present than in summer communities in the same lakes. Certain species (e.g. *Diaptomus sicilis*) while present the year round in some lakes (e.g. Patricia and Pyramid lakes) were absent during winter in others (e.g. Little Herbert and Thurston's T-2). Year round presence was apparently due to a 12-mo generation time in the former lakes, whereas the generation time was less than 6 mo in the latter. *Daphnia catawba* was found only in winter samples from a few lakes, although most *Daphnia* spp. populations were restricted to the ice-free period. Sampling in winter has not shown the widespread occurrence of distinctly different winter crustacean plankton communities in the study area, except for lakes yielding *D. catawba* in winter but rarely, if at all, during the ice-free period, and one lake (Kingfisher, Banff N.P.) which contained *Diaptomus leptopus* in summer and *Acanthodiaptomus denticornis* in winter.

Most *Hesperodiaptomus* spp. populations were present only in summer, although they are known to persist throughout the year in a few lakes (e.g. Horseshoe Lake, Banff). As noted above and elsewhere (Anderson 1970c), when certain *Hesperodiaptomus* spp. occur in shallow prairie lakes and ponds, they may mature and produce eggs within two months of the spring thaw and then disappear for the remainder of the open water season, well before the summer community is fully developed. *Diaptomus arcticus*, *D. tyrrelli*, and *Branchinecta paludosa* are three species that seem especially well adapted to take advantage of the brief period of suitable environmental conditions that occur in prairie waters, yet they can take up to four times as long to develop in cold, oligotrophic waters. This is perhaps why they are the most abundant and frequently occurring species among the calanoid copepods and the Anostraca.

Patterns of regional distribution were evident for only a few species. *D. arapahoensis* occurred only in Waterton Lakes National Park waters and in a few mountain lakes between this park and Banff National Park. *D. shoshone* occurred in the same region and in many lakes in south and central Jasper National Park. *D. shoshone* is known from lakes west of Jasper in British Columbia (Carl 1940) and both species are known from high altitude lakes in Colorado (Reed and Olive 1956). *Hopopedium gibberum* occurred most frequently in the same region as *D. shoshone*, but was also abundant in the few lakes and ponds in Glacier and Mt. Revelstoke National Parks. The salinity range in which *H. gibberum* occurred was 2–52 ppm. These three species seem to be confined to low-salinity, high-altitude lakes in the study area, many of the lakes being very deep and clear. In spite of the similarities in regional distribution, *H. gibberum* was found with *D. shoshone* in only 6 of 20 occurrences. Patalas (1971) found *H. gibberum* only in shallow, low-transparency ELA lakes; Mayhood et al. (1973) found *H. gibberum* in high calcium, hard water lakes (TDS = total dissolved solids = 167 ppm). As noted by Carl (1940), this species may be more widely distributed than originally thought, and its distribution may be limited by factors other than TDS, calcium, or pH in many waters. Many early references to *D. shoshone*, especially in high salinity, shallow waters, were very likely to *D. nevadensis*. Consequently, the tolerance range of this species is difficult to assess from the literature.

Acanthodiaptomus denticornis lakes (Table 5) included a fairly wide range of environmental conditions, but in the region where it occurred, the species was absent from the very high-altitude s and ponds.[a]

Ceriodaphnia affinis	*Ceriodaphnia recticulata*	*Ceriodaphnia acanthina*	*Ceriodaphnia quadrangula*	*Moina macrocopa*	*Bosmina longirostris*	*Eurycercus lamellatus*	*Diaptomus novemdecimus*	*Diaptomus hirsutus*	*Diaptomus nevadensis*	*Diaptomus arcticus*	*Diaptomus breweri*	*Diaptomus leptopus*	*Diaptomus forbesi*	*Diaptomus tyrrelli*	*Diaptomus sicilis*	*Diaptomus nudus*	*Diaptomus assiniboiaensis*	*Diaptomus sanguineus*	*Orthocyclops modestus*	*Macrocyclops albidus*	*Eucyclops agilis*	*Eucyclops speratus*	*Acanthocyclops vernalis*	*Diacyclops nanus*	*Diacyclops bicuspidatus thomasi*	*Microcyclops varicans rubellus*	*Canthocamptus oregonensis*	*Bryocamptus zschokkei*	*Branchinecta gigas*	*Branchinecta mackini*	*Branchinecta paludosa*	*Eubranchipus intricatus*	*Streptocephalus seali*	*Lynceus brachyurus*	*Lepidurus lynchi*	*Lepidurus apus*	*Gammarus lacustris*	*Hyalella azteca*
.	.	.	.	.	.	.	.	.	.	2	.	.	.	3	.	.	.	.	.	.	.	.	2?•	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.
.	.	.	.	.	.	.	.	.	.	2	.	.	.	3	.	.	.	.	.	.	.	.	2?•	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.
.	.	.	.	.	.	.	.	.	.	2	.	.	.	4	.	.	.	.	.	.	.	.	2?•	.	.	.	1?•	.	.	.	.	.	.	.	.	.	.	.
.	.	.	.	.	.	.	.	.	.	2	.	.	.	2	.	.	.	.	.	.	.	.	3?•	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
.	.	.	.	.	.	.	.	.	.	3	.	.	.	4	.	.	.	.	.	.	.	.	2?•	.	.	.	.	.	.	.	2	.	.	.	.	.	.	.
.	.	.	.	.	.	1	.	.	.	3	.	.	.	4	.	.	.	.	.	.	.	.	3	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
.	.	.	.	.	.	.	.	.	.	1	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
.	.	.	.	.	.	.	.	.	.	2	.	.	.	2	.	.	.	.	.	.	.	.	.	.	3	.	.	.	.	.	.	.	.	.	.	.	.	.
.	.	.	.	.	.	.	.	.	.	1	.	.	.	2	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.
.	.	.	.	.	.	.	.	.	.	2	.	.	.	2	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
.	.	.	.	.	.	.	.	.	.	1	.	.	.	.	3	.	.	.	.	.	1	.	2	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
.	.	.	.	.	.	.	.	.	.	2	.	.	.	3	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
.	.	.	.	.	.	.	.	.	.	2	.	.	.	3	.	.	.	.	.	.	.	.	2	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
.	.	.	.	.	.	.	.	.	.	2	.	.	.	3	.	.	.	.	.	.	.	.	2	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
.	.	.	.	.	.	.	.	.	.	3	.	.	.	4	.	.	.	.	.	.	.	.	1?•	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
.	.	.	.	.	.	.	.	.	.	2	.	.	.	4	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
.	.	.	.	.	.	.	.	.	.	2	.	.	.	3	.	.	.	.	.	.	.	.	2?•	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
.	.	.	.	.	.	.	.	.	.	1	.	.	.	.	2	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
.	.	.	.	.	1	.	.	.	.	2	.	.	.	.	4	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
.	.	.	.	.	.	.	.	.	.	2	.	.	.	3	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
.	3	.	.	.	.	.	.	.	.	1	.	.	.	5	.	.	.	.	.	.	.	.	3	.	.	.	.	.	.	.	.	.	2?•	.	.	.	.	.
.	.	2	.	.	.	.	.	.	.	2	.	.	2	4	.	2	.	.	.	2	2	.	2	.	.	.	.	.	.	.	.	.	.	.	.	.	1	1
2	.	.	.	.	.	.	.	.	.	1	.	.	2	3	.	4	.	.	.	2	2	.	3	.	2	.	.	.	.	.	.	.	.	.	.	.	1	1
.	.	3	2	.	.	.	.	.	.	3	.	.	2	4	.	2	.	3	.	.	2	.	4	.	3	3	2	.	.	.	.	.	.	2	.	.	.	.
.	.	.	.	.	.	.	.	.	.	3	.	.	.	.	.	.	.	.	.	.	.	.	1	.	2	.	.	1	.	.	.	.	.	.	.	.	.	.
.	.	.	.	.	.	.	.	.	.	2	.	.	.	.	.	.	.	.	.	.	.	.	.	.	2	.	.	.	.	.	.	.	.	.	.	.	.	.
.	.	.	.	.	.	.	.	.	.	3	.	.	.	.	.	.	.	.	.	.	.	.	3	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
.	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.
.	.	.	.	.	.	.	.	.	.	3	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.
.	.	.	.	.	.	.	.	.	.	3	.	.	.	.	.	.	.	.	.	.	.	.	1?•	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
.	.	.	.	.	.	.	.	.	.	3	.	.	.	.	.	.	.	.	.	.	.	.	2?•	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
.	.	.	.	.	.	.	.	.	.	2	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
.	.	.	.	.	.	.	.	.	.	3	.	.	.	.	.	.	.	.	.	.	.	.	2?•	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
.	.	.	.	.	.	.	.	.	.	2	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.
.	.	.	.	.	.	.	.	.	.	3	.	.	.	.	.	.	.	.	.	.	1	1	1	.	2	.	1	.	.	.	.	.	.	.	.	.	.	.
.	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	2	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
.	.	.	.	.	.	.	.	.	.	3	.	.	.	.	.	.	.	.	1	.	.	.	3	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
.	.	.	.	.	.	.	.	.	.	3	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.
.	.	.	.	.	.	.	.	.	.	4	.	.	.	.	.	.	.	.	.	.	.	.	1	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.
.	.	.	.	.	.	.	.	.	.	3	.	.	.	.	.	.	.	.	.	.	.	.	2?•	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
.	.	.	.	.	.	.	.	.	.	3	.	.	.	.	.	.	.	.	.	.	.	.	.	.	2	.	.	.	.	.	.	.	.	.	.	.	.	.
.	.	.	.	.	.	.	.	.	.	3	.	.	.	.	.	.	.	.	.	.	.	.	3	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
.	.	.	.	.	.	.	.	.	.	3	.	.	.	.	.	.	.	.	.	.	.	2	2	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.
.	.	.	.	.	.	.	.	.	.	2	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
.	.	.	.	.	.	.	.	.	.	3	.	.	.	.	.	.	.	.	.	.	2	.	2	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.
.	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.
.	.	.	.	.	.	.	.	.	.	3	.	.	.	.	.	.	.	.	2	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.
.	.	.	.	.	.	.	.	.	.	2	.	.	.	.	.	.	.	.	.	.	.	.	1?•	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
.	3	.	.	.	.	.	.	.	.	.	3	5	.	.	.	.	3	4	.	.	.	.	2	.	.	.	.	.	.	.	.	.	3	.	.	.	.	.
.	.	.	3	.	.	.	.	.	.	3	.	2	.	.	.	5	.	.	.	2	2	.	3	.	.	3	1?•	.	.	.	.	.	.	.	.	.	.	.
.	.	.	.	.	.	.	.	.	.	3	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	2?•	.	.	.	.	.	.	.
.	.	.	.	.	.	.	.	.	4	.	.	.	.	.	5	.	.	.	.	.	.	.	.	.	.	.	.	.	.	3	.	.	.	.	.	1	.	.
.	.	.	.	.	.	.	.	.	3	.	.	.	.	.	4	.	.	.	.	.	.	.	.	.	.	.	.	.	2	3	.	.	.	.	.	1	.	.
.	.	.	.	1	.	.	.	.	3	.	.	.	.	.	5	.	.	.	.	.	.	.	1?•	.	.	.	.	.	2	.	.	.	.	1	1	.	.	.
.	.	.	.	.	.	.	.	.	3	.	.	.	3	.	4	.	.	.	.	1	.	.	3	.	.	.	.	.	.	.	.	.	.	.	.	.	3	.
.	.	.	.	.	.	.	.	.	4	.	.	.	.	.	5	.	.	.	.	.	.	.	.	.	.	.	.	.	2	4	.	.	.	.	.	.	.	.
3	.	.	1	.	.	.	3	.	.	.	.	.	.	.	.	.	.	4	.	.	.	.	3	3	.	3	2	.	.	.	.	2	.	1?•	.	.	.	.
.	.	.	.	.	.	.	.	3	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	3	.	.	.	.	.	.	.	.	.	.	.	.	.	.

Lake No.	Name	Grid reference	Date for chem data	Elevation (*m*)	Area (*ha*)	Max known depth (*m*)	Secchi disc depth (*m*) max found	pH
B 180	Lost L.	11U/NH505026	25.6.70	1723	1.6	5.5	+^{d}	8.2
B 169	Mud L.	11U/NG573989	25.6.70	1610	6.0	6.0	+^{d}	8.5
B 165	Island L.	11U/NG618935	29.8.69	1573	12.5	5.0	+^{d}	8.6
B 79	Smith L.	11U/NG751779	31.8.70	1560	3.0	9.7	8.6	8.4
B 78	Copper L.	11U/NG753791	25.6.70	1434	1.5	9.0	8.6	8.6
B 475	Pilot P.	11U/NG830757	24.6.70	1408	2.8	7.5	6.5	8.8
B 183	Herbert P.	11U/NH541007	2.6.70	1615	0.3	1.5	+^{d}	8.1
B 182	Herbert L.	11U/NH542010	22.8.67	1615	5.7	13.3	12.6	8.3
B 184	Little Herbert	11U/NH546001	20.8.72	1577	0.3	8.2	7.0	7.8
B 167	Kingfisher L.	11U/NG583956	25.6.70	1550	1.0	7.2	+^{d}	8.4
A	Pigeon L.	11U/PG265570	25.6.70	1243	7.0	2.4	+^{d}	8.5
P	Glenmore Res.	11U/QG025520	3.10.70	1071	400.0	18.3	2.0	–
P	Church Pond B	11U/PG909726	.7.69	1241	<0.1	0.6	+^{d}	9.0
B 73	Johnson L.	11U/PG058726	23.6.70	1402	12.0	3.5	+^{d}	8.4
J 194	Moab L.	11U/MJ355347	18.6.70	1204	22.0	18.5	12.5	8.0
J 277	Lorraine L.	11U/MJ550422	15.7.70	1740	2.5	8.2	+^{d}	8.5
J 392	Tekarra Ck. P.	11U/MJ292558	6.6.69	1098	0.2	1.5	+^{d}	–
J 390	Mildred L.	11U/MJ289603	6.6.68	1033	6.0	3.5	+^{d}	–
J 394	Trefoil #3 P	11U/MJ288605	30.9.70	1027	0.3	5.5	+^{d}	8.2
J 410	Caledonia L.	11U/MJ218578	30.9.70	1160	16.0	10.5	6.0	7.8
J 408	Hibernia L.	11U/MJ231583	17.6.70	1198	10.0	9.0	+^{d}	8.2
J 582	Celestine L.	11U/MJ301934	.8.68	1260	39.0	14.0	14.0	8.5
J 581	Princess L.	11U/MJ287937	17.6.70	1244	36.0	4.5	+^{d}	8.4
J 759	S. Twin L.	11U/MJ280578	31.7.66	1033	1.0	11.5	+^{d}	8.1
J 423	Virl L.	11U/MJ170592	17.7.70	1305	4.5	6.0	5.3	8.5
J 421	Lily P.	11U/MJ174592	17.7.70	1323	0.8	4.0	4.0	8.0
J 278	Mona L.	11U/MJ545430	15.7.70	1750	11.0	10?	+^{d}	8.5
J 144	Buck L.	11U/MJ553223	18.6.70	1405	14.0	6.0	+^{d}	8.6
J 422	Dorothy L.	11U/MJ172597	18.7.68	1335	27.0	16.0	6.0	8.7
J 426	Christine L.	11U/MJ166600	18.7.70	1338	7.0	8.4	6.0	8.4
J 407	Marjorie L.	11U/MJ239579	21.8.70	1143	6.0	7.5	+^{d}	8.3
J 388	Trefoil #1 L.	11U/MJ291608	29.9.70	1030	3.5	10.0	9.2	8.3
J 760	N. Twin L.	11U/MJ279582	21.8.68	1033	1.0	1.5	+^{d}	8.0
J 297	16½-Mile L. U.	11U/MJ386400	18.6.70	1174	5.5	6.0	5.3	8.3
J 292	Leach P #2	11U/MJ398360	18.6.70	1200	1.0	1.0	+^{d}	8.4
J 145	Honeymoon L.	11U/MJ542228	18.6.70	1405	15.0	6.5	+^{d}	8.4
J 800	Palisades P.	11U/MJ295685	29.8.69	1027	0.4	1.0	+^{d}	8.7
J 588	Pocahontas P.	11U/MJ387957	29.8.69	1003	3.0	2.0	0.5	8.3
J 406	Cabin L.	11U/MJ240590	17.6.70	1210	32.0	20.5	8.5	8.0
J 403	Mina L.	11U/MJ247597	17.6.70	1214	7.0	13.0	8.7	8.5
J 332	5th of five	11U/MJ325518	14.7.70	1143	6.5	13.0	8.0	8.3
W 18	Linnet L.	12U/TK878382	27.9.72	1280	3.0	4.7	+^{d}	8.3
W 52	Ruby L.	11U/QE177419	10.8.71	2064	2.0	12.0	+^{d}	8.3
W 31	Beaver P. 31	12U/TK997380	8.6.71	1524	2.0	3.0	+^{d}	8.2
W 51	Kesler	12U/TK860518	29.6.71	1503	10.0	2.0	+^{d}	8.2
W 61	Pond 61	12U/TK926438	1.8.72	1276	0.8	1.5	+^{d}	7.6
W 21	Lonesome L.	12U/TK889395	23.7.70	1280	6.5	3.0	+^{d}	9.5
W 43	Maskinonge L.	12U/TK930431	9.8.71	1276	65.0	1.0	+^{d}	8.2
A	Bear L.	11U/PF834658	27.8.66	1800	2.0	4.0	2.0	7.3
A	Hartell Res.	11U/PG937073	3.6.69	1234	14.0	4.0	1.0	8.4
K 18	Kootenay P.	11U/NG675381	9.8.72	1213	3.0	7.5	6.0	8.1
K 24	Little Kootenay P.	11U/NG672383	11.6.70	1214	0.5	6.8	+^{d}	9.0
K 6	Nixon P.	11U/NG754211	15.6.70	1183	2.5	1.0	+^{d}	8.8
K 5	Dog L.	11U/NG756258	12.6.70	1183	12.0	3.5	+^{d}	8.3
W 45	Buffalo L.	12U/TK916456	4.6.71	1329	10.5	3.6	+^{d}	8.4
W 48B	Indian springs P.	12U/TK901456	6.6.70	1351	0.2	1.0	+^{d}	8.4
W 44	Buffalo Ck. P.	12U/TK918454	4.6.71	1323	0.8	1.5	+^{d}	9.0

[a] Footnotes as in Table 4.

TABLE 5. Crustacean plankton density, species composition and abundance, and some limnological features for 57 Group IV lakes and ponds.[a]

TDS[c,d] (*ppm*)	Heat content (*kcal*)	Crustacean plankton				*Leptodora kindtii*	*Polyphemus pediculus*	*Sida crystallina*	*Latona setifera*	*Diaphanosoma brachyurum*	*Diaphanosoma leuchtenbergianum*	*Eurycercus lamellatus*	*Acroperus harpae*	*Graptoleberis testudinaria*	*Alona guttata*	*Alona affinis*	*Alona costata*	*Alona rectangula*	*Alona intermedia*	*Alona quadrangularis*	*Alonella nana*	*Alonella exigua*	*Chydorus sphaericus*	*Pleuroxus denticulatus*	*Pleuroxus trigonellus*	*Daphnia magna*	*Daphnia longiremis*	*Daphnia rosea*	*Daphnia galeata mendotae*	*Daphnia middendorffiana*	*Daphnia pulex*	
		Max no. per liter	Total no. spp.	Cladocera spp.	Copepoda spp.																											
163	18.6	65.0	7	4	3	.	3	.	.	.	.	.	.	.	1 ?[e]	.	.	.	.	.	.	.	.	.	.	.	.	2	.	.	.	
158	15.8	70.0	5	3	2	.	3	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	
124	18.4	13.2	6	3	2	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.	4	
173	14.1	75.0	7	4	3	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	4	.	.	
86	14.2	35.0	6	4	2	.	2	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	3	.	.	.	
202	14.7	45.0	3	1	2	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	4	
127	17.6	25.0	7	4	2	.	2	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.	4 ?[e]	
173	16.7	107.6	16	10	6	.	2	.	.	.	.	1	.	.	.	.	.	1	.	.	.	.	1	.	.	.	.	3 ?[e]	1 ?[e]	.	.	
185[f]	16.0	110.4	12	6	6	.	2	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.	4	.	.	.	
118	18.8	55.0	11	7	4	.	2	.	.	.	.	.	.	.	1	.	.	.	1	.	.	.	1	.	.	.	.	.	.	.	3	
139	16.7	75.0	5	3	2	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	2 ?[e]	
–	15.0[b]	45.0	10	6	4	.	.	2	.	.	2	.	.	.	.	.	.	.	.	.	.	.	3	2	.	.	.	.	.	.	2	
560[f]	22.0[b]	400+	19	8	6	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	5	.	3	4	.	3	.	.	5	
165	17.7	95.0	10	6	4	.	.	.	.	.	.	2	2	.	.	.	.	.	.	.	3	.	2	.	.	.	.	4	.	.	.	
80	8.8	16.8	8	4	4	.	1	.	.	2	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	
65	14.1	19.3	6	5	1	.	2	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.	
–	13.9	110.0	5	2	2	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	3	.	.	.	
–	20.0[b]	300.0	10	5	4	.	3	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.	2	.	.	.	.	.	.	.	.	
151	18.0[b]	92.8	6	3	3	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.	1	.	.	.	.	.	.	.	.	3
62	9.4	97.4	8	5	3	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	.	3	4	.	.	.	
143	15.4	24.6	8	5	3	.	1	.	.	2	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.	
138	14.5	39.1	18	13	4	.	1	.	.	.	.	.	.	1	1	.	.	1	.	.	1	.	1	.	.	.	.	.	1 ?[e]	.	4	
191	16.4	27.2	6	2	4	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	4
126	18.3	23.0	11	7	4	.	2	.	.	.	.	.	.	.	.	.	.	.	.	.	3	.	2	.	.	.	.	2	.	.	.	
104	18.8	139.2	7	5	2	.	.	.	.	.	3	.	.	.	.	.	.	.	.	.	.	.	2	.	.	.	.	4	.	.	.	
63	18.0	18.7	8	3	3	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	3	.	.	.	.	.	.	.	3 ?[e]	
105	15.6	6.7	5	3	2	.	2	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	
87	15.5	8.0	8	6	2	.	1	.	.	.	2	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	
145	13.6	79.2	16	10	6	.	1	.	.	.	2	.	.	.	1	.	.	.	.	.	1	.	1	.	.	.	.	3	.	.	.	
118	17.4	76.7	9	6	3	.	.	.	.	.	2	.	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.	3	.	.	.	
155	15.2	38.7	9	6	3	.	2	.	.	.	2	.	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.	3	.	.	3 ?[e]	
182	10.3	12.2	7	2	5	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	3	
120	15.5	35.0	11	6	5	.	3	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.	4	.	.	.	.	2 ?[e]	.	.	.	
160	15.8	29.3	10	5	5	.	2	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	2	.	.	.	.	.	.	.	.	
134	23.0[b]	123.1	6	3	3	.	2	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	3	.	.	.	.	.	.	.	.	
93	15.5	38.3	10	6	4	.	1	.	.	.	2	.	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.	.	3
140	19.1	200.0	12	7	5	.	2	.	.	2	.	.	.	.	.	.	.	.	.	2	.	.	3	.	.	.	.	4	.	.	.	
229	13.6	45.0	12	7	4	.	2	.	.	3	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.	3	.	.	4	
84	8.2	12.2	10	6	4	1	1	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	2 ?[e]	.	.	
357[e]	9.8	25.3	8	5	3	.	2	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.	.	
166[e]	16.1	46.9	5	2	3	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	
104	21.4	600.0	10	5	4	.	.	.	.	.	.	.	.	.	3	.	.	.	2	.	.	.	3	.	.	.	.	.	.	.	.	
91	15.8	9.0	4	1	3	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1 ?[e]	
192	13.6	60.0	11	6	5	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.	.	3	.	.	.	.	2	.	.	2	
105	14.1	187.8	8	5	3	.	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.	2	.	.	.	.	.	.	.	3	
140	16.3	120.0	15	10	4	.	3	.	.	1	.	2	.	.	.	1	.	.	.	.	.	.	2	3	.	.	.	2	.	.	.	
76	18.8	175.0	13	8	5	.	.	.	.	.	.	.	.	.	2	.	.	.	2	.	3	.	4	.	.	.	.	.	.	.	.	
204	26.7	188.0	25	17	7	.	3	2	2	2	.	2	3	1	1	.	.	.	.	.	.	2	2	.	.	.	.	2	.	1	.	
30	17.3	150.0	8	3	3	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	2	.	.	.	.	.	.	.	.	
306	21.0[b]	90.0	12	7	5	.	.	.	.	.	.	.	.	.	2	.	.	.	.	.	.	.	2	.	.	.	.	3	4	.	.	
237	18.8	74.0	6	3	3	.	.	.	.	3	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	4	
161	16.7	61.7	6	2	3	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	4	
117	15.9	50.0	8	6	2	.	.	.	.	1	.	1	.	.	.	.	.	.	.	.	.	.	2	.	.	.	.	4	.	.	.	
163	15.9	168.1	10	8	2	.	2	.	.	.	2	.	.	.	.	.	.	.	.	.	.	.	2	.	.	.	.	4	.	.	.	
165	23.0[b]	277.3	8	4	4	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	3	.	.	.	.	.	.	.	4	
206a	26.0	663.5	10	3	5	.	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	
131	23.0	208.8	19	12	6	.	.	.	.	.	.	.	.	.	.	2	.	.	1	.	3	.	3	.	.	.	.	1	.	.	.	

Lake No.	Name	Grid reference	Date for chem data	Elevation (m)	Area (ha)	Max known depth (m)	Secchi disc depth (m) max found
B 180	Lost L.	11U/NH505026	25.6.70	1723	1.6	5.5	+^{d}
B 169	Mud L.	11U/NG573989	25.6.70	1610	6.0	6.0	+^{d}
B 165	Island L.	11U/NG618935	29.8.69	1573	12.5	5.0	+^{d}
B 79	Smith L.	11U/NG751779	31.8.70	1560	3.0	9.7	8.6
B 78	Copper L.	11U/NG753791	25.6.70	1434	1.5	9.0	8.6
B 475	Pilot P.	11U/NG830757	24.6.70	1408	2.8	7.5	6.5
B 183	Herbert P.	11U/NH541007	2.6.70	1615	0.3	1.5	+^{d}
B 182	Herbert L.	11U/NH542010	22.8.67	1615	5.7	13.3	12.6
B 184	Little Herbert	11U/NH546001	20.8.72	1577	0.3	8.2	7.0
B 167	Kingfisher L.	11U/NG583956	25.6.70	1550	1.0	7.2	+^{d}
A	Pigeon L.	11U/PG265570	25.6.70	1243	7.0	2.4	+^{d}
P	Glenmore Res.	11U/QG025520	3.10.70	1071	400.0	18.3	2.0
P	Church Pond B	11U/PG909726	.7.69	1241	<0.1	0.6	+^{d}
B 73	Johnson L.	11U/PG058726	23.6.70	1402	12.0	3.5	+^{d}
J 194	Moab L.	11U/MJ355347	18.6.70	1204	22.0	18.5	12.5
J 277	Lorraine L.	11U/MJ550422	15.7.70	1740	2.5	8.2	+^{d}
J 392	Tekarra Ck. P.	11U/MJ292558	6.6.69	1098	0.2	1.5	+^{d}
J 390	Mildred L.	11U/MJ289603	6.6.68	1033	6.0	3.5	+^{d}
J 394	Trefoil #3 P	11U/MJ288605	30.9.70	1027	0.3	5.5	+^{d}
J 410	Caledonia L.	11U/MJ218578	30.9.70	1160	16.0	10.5	6.0
J 408	Hibernia L.	11U/MJ231583	17.6.70	1198	10.0	9.0	+^{d}
J 582	Celestine L.	11U/MJ301934	.8.68	1260	39.0	14.0	14.0
J 581	Princess L.	11U/MJ287937	17.6.70	1244	36.0	4.5	+^{d}
J 759	S. Twin L.	11U/MJ280578	31.7.66	1033	1.0	11.5	+^{d}
J 423	Virl L.	11U/MJ170592	17.7.70	1305	4.5	6.0	5.3
J 421	Lily P.	11U/MJ174592	17.7.70	1323	0.8	4.0	4.0
J 278	Mona L.	11U/MJ545430	15.7.70	1750	11.0	10?	+^{d}
J 144	Buck L.	11U/MJ553223	18.6.70	1405	14.0	6.0	+^{d}
J 422	Dorothy L.	11U/MJ172597	18.7.68	1335	27.0	16.0	6.0
J 426	Christine L.	11U/MJ166600	18.7.70	1338	7.0	8.4	6.0
J 407	Marjorie L.	11U/MJ239579	21.8.70	1143	6.0	7.5	+^{d}
J 388	Trefoil #1 L.	11U/MJ291608	29.9.70	1030	3.5	10.0	9.2
J 760	N. Twin L.	11U/MJ279582	21.8.68	1033	1.0	1.5	+^{d}
J 297	16½-Mile L. U.	11U/MJ386400	18.6.70	1174	5.5	6.0	5.3
J 292	Leach P #2	11U/MJ398360	18.6.70	1200	1.0	1.0	+^{d}
J 145	Honeymoon L.	11U/MJ542228	18.6.70	1405	15.0	6.5	+^{d}
J 800	Palisades P.	11U/MJ295685	29.8.69	1027	0.4	1.0	+^{d}
J 588	Pocahontas P.	11U/MJ387957	29.8.69	1003	3.0	2.0	0.5
J 406	Cabin L.	11U/MJ240590	17.6.70	1210	32.0	20.5	8.5
J 403	Mina L.	11U/MJ247597	17.6.70	1214	7.0	13.0	8.7
J 332	5th of five	11U/MJ325518	14.7.70	1143	6.5	13.0	8.0
W 18	Linnet L.	12U/TK878382	27.9.72	1280	3.0	4.7	+^{d}
W 52	Ruby L.	11U/QE177419	10.8.71	2064	2.0	12.0	+^{d}
W 31	Beaver P. 31	12U/TK997380	8.6.71	1524	2.0	3.0	+^{d}
W 51	Kesler	12U/TK860518	29.6.71	1503	10.0	2.0	+^{d}
W 61	Pond 61	12U/TK926438	1.8.72	1276	0.8	1.5	+^{d}
W 21	Lonesome L.	12U/TK889395	23.7.70	1280	6.5	3.0	+^{d}
W 43	Maskinonge L.	12U/TK930431	9.8.71	1276	65.0	1.0	+^{d}
A	Bear L.	11U/PF834658	27.8.66	1800	2.0	4.0	2.0
A	Hartell Res.	11U/PG937073	3.6.69	1234	14.0	4.0	1.0
K 18	Kootenay P.	11U/NG675381	9.8.72	1213	3.0	7.5	6.0
K 24	Little Kootenay P.	11U/NG672383	11.6.70	1214	0.5	6.8	+^{d}
K 6	Nixon P.	11U/NG754211	15.6.70	1183	2.5	1.0	+^{d}
K 5	Dog L.	11U/NG756258	12.6.70	1183	12.0	3.5	+^{d}
W 45	Buffalo L.	12U/TK916456	4.6.71	1329	10.5	3.6	+^{d}
W 48B	Indian springs P.	12U/TK901456	6.6.70	1351	0.2	1.0	+^{d}
W 44	Buffalo Ck. P.	12U/TK918454	4.6.71	1323	0.8	1.5	+^{d}

---

[a] Footnotes as in Table 4.

4

TABLE 5. Crustacean plankton density, species composition and abundance, and some limnological features for 57 Group IV lakes and ponds.[a]

pH	TDS[**] (ppm)	Heat content (kcal)	Crustacean plankton				Leptodora kindtii	Polyphemus pediculus	Sida crystallina	Latona setifera	Diaphanosoma brachyurum	Diaphanosoma leuchtenbergianum	Eurycercus lamellatus	Acroperus harpae	Graptoleberis testudinaria	Alona guttata	Alona affinis	Alona costata	Alona rectangula	Alona intermedia	Alona quadrangularis	Alonella nana	Alonella exigua	Chydorus sphaericus	Pleuroxus denticulatus	Pleuroxus trigonellus	Daphnia magna	Daphnia longiremis	Daphnia rosea	Daphnia galeata mendotae	Daphnia middendorffiana	Daphnia pulex
			Max no. per liter	Total no. spp.	Cladocera spp.	Copepoda spp.																										
.2	163	18.6	65.0	7	4	3	.	3	.	.	.	.	.	.	.	1 ?[e]	.	.	.	.	.	.	.	.	.	.	.	.	2	.	.	.
.5	158	15.8	70.0	5	3	2	.	3	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
.6	124	18.4	13.2	6	3	2	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.	4
.4	173	14.1	75.0	7	4	3	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	4	.	.
.6	86	14.2	35.0	6	4	2	.	2	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	3	.	.	.
.8	202	14.7	45.0	3	1	2	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	4
.1	127	17.6	25.0	7	4	2	.	2	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.	4 ?[e]
.3	173	16.7	107.6	16	10	6	.	2	.	.	.	.	1	.	.	.	.	.	1	.	.	.	.	1	.	.	.	.	3 ?[e]	1 ?[e]	.	.
7.8	185[f]	16.0	110.4	12	6	6	.	2	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.	4	.	.	.
.4	118	18.8	55.0	11	7	4	.	2	.	.	.	.	.	.	.	1	.	.	.	1	.	.	.	1	.	.	.	.	.	.	.	3
.5	139	16.7	75.0	5	3	2	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	2 ?[e]
–	–	15.0[b]	45.0	10	6	4	.	.	2	.	.	2	.	.	.	.	.	.	.	.	.	.	.	3	2	.	.	.	.	.	.	2
.0	560[f]	22.0[b]	400+	19	8	6	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	5	.	3	4	.	3	.	.	5
.4	165	17.7	95.0	10	6	4	.	.	.	.	.	.	2	2	.	.	.	.	.	.	.	3	.	2	.	.	.	.	4	.	.	.
.0	80	8.8	16.8	8	4	4	.	1	.	.	2	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
.5	65	14.1	19.3	6	5	1	.	2	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.
–	–	13.9	110.0	5	2	2	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	3	.	.	.
–	–	20.0[b]	300.0	10	5	4	.	3	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.	2	.	.	.	.	.	.	.	.
.2	151	18.0[b]	92.8	6	3	3	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.	1	.	.	.	.	.	.	.	.
7.8	62	9.4	97.4	8	5	3	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	.	3	4	.	.	.
.2	143	15.4	24.6	8	5	3	.	1	.	.	2	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.
.5	138	14.5	39.1	18	13	4	.	1	.	.	.	.	.	.	1	1	.	.	1	.	.	1	.	1	.	.	.	.	.	1 ?[e]	.	4
.4	191	16.4	27.2	6	2	4	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
.1	126	18.3	23.0	11	7	4	.	2	.	.	.	.	.	.	.	.	.	.	.	.	.	3	.	2	.	.	.	.	2	.	.	.
.5	104	18.8	139.2	7	5	2	.	.	.	.	.	3	.	.	.	.	.	.	.	.	.	.	.	2	.	.	.	.	4	.	.	.
.0	63	18.0	18.7	8	3	3	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	3	.	.	.	.	.	.	.	3 ?[e]
.5	105	15.6	6.7	5	3	2	.	2	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
.6	87	15.5	8.0	8	6	2	.	1	.	.	.	2	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
.7	145	13.6	79.2	16	10	6	.	1	.	.	.	2	.	.	.	1	.	.	.	.	.	1	.	1	.	.	.	.	3	.	.	.
.4	118	17.4	76.7	9	6	3	.	.	.	.	.	2	.	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.	3	.	.	.
.3	155	15.2	38.7	9	6	3	.	2	.	.	.	2	.	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.	3	.	.	3 ?[e]
.3	182	10.3	12.2	7	2	5	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	3
.0	120	15.5	35.0	11	6	5	.	3	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.	4	.	.	.	.	2 ?[e]	.	.	.
.3	160	15.8	29.3	10	5	5	.	2	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	2	.	.	.	.	.	.	.	.
.4	134	23.0[b]	123.1	6	3	3	.	2	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	3	.	.	.	.	.	.	.	.
.4	93	15.5	38.3	10	6	4	.	1	.	.	.	2	.	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.	.
.7	140	19.1	200.0	12	7	5	.	2	.	.	2	.	.	.	.	.	.	.	.	.	2	.	.	3	.	.	.	.	4	.	.	.
.3	229	13.6	45.0	12	7	4	.	2	.	.	3	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.	3	.	.	4
.0	84	8.2	12.2	10	6	4	1	1	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	2 ?[e]	.	.
.5	357[e]	9.8	25.3	8	5	3	.	2	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.	.
.3	166[e]	16.1	46.9	5	2	3	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
.3	104	21.4	600.0	10	5	4	.	.	.	.	.	.	.	.	.	3	.	.	.	2	.	.	.	3	.	.	.	.	.	.	.	.
.3	91	15.8	9.0	4	1	3	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1 ?[e]
.2	192	13.6	60.0	11	6	5	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.	.	3	.	.	.	.	2	.	.	2
.2	105	14.1	187.8	8	5	3	.	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.	2	.	.	.	.	.	.	.	3
7.6	140	16.3	120.0	15	10	4	.	3	.	.	1	.	2	.	.	.	1	.	.	.	.	.	.	2	3	.	.	.	2	.	.	.
.5	76	18.8	175.0	13	8	5	.	.	.	.	.	.	.	.	.	2	.	.	.	2	.	3	.	4	.	.	.	.	.	.	.	.
.2	204	26.7	188.0	25	17	7	.	3	2	2	2	.	2	3	1	1	.	.	.	.	.	.	2	2	.	.	.	.	2	.	1	.
7.3	30	17.3	150.0	8	3	3	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	2	.	.	.	.	.	.	.	.
.4	306	21.0[b]	90.0	12	7	5	.	.	.	.	.	.	.	.	.	2	.	.	.	.	.	.	.	2	.	.	.	.	3	4	.	.
.1	237	18.8	74.0	6	3	3	.	.	.	.	3	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	4
.0	161	16.7	61.7	6	2	3	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	4
.8	117	15.9	50.0	8	6	2	.	.	.	.	1	.	1	.	.	.	.	.	.	.	.	.	.	2	.	.	.	.	4	.	.	.
.3	163	15.9	168.1	10	8	2	.	2	.	.	.	2	.	.	.	.	.	.	.	.	.	.	.	2	.	.	.	.	4	.	.	.
.4	165	23.0[b]	277.3	8	4	4	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	3	.	.	.	.	.	.	.	4
.4	206a	26.0	663.5	10	3	5	.	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.
.0	131	23.0	208.8	19	12	6	.	.	.	.	.	.	.	.	.	.	2	.	.	1	.	3	.	3	.	.	.	.	1	.	.	.

5

Daphnia pulicaria	*Daphnia schoedleri*	*Daphnia parvula*	*Simocephalus vetulus*	*Simocephalus serrulatus*	*Scapholeberis kingi*	*Ceriodaphnia affinis*	*Ceriodaphnia reticulata*	*Ceriodaphnia acanthina*	*Ceriodaphnia lacustris*	*Ceriodaphnia pulchella*	*Ceriodaphnia quadrangula*	*Bosmina longirostris*	*Acanthodiaptomus denticornis*	*Diaptomus leptopus*	*Diaptomus forbesi*	*Diaptomus tyrrelli*	*Diaptomus sicilis*	*Diaptomus nudus*	*Orthocyclops modestus*	*Macrocyclops albidus*	*Eucyclops agilis*	*Eucyclops speratus*	*Acanthocyclops vernalis*	*Diacyclops navus*	*Diacyclops bicuspidatus thomasi*	*Microcyclops varicans rubellus*	*Canthocamptus oregonensis*	*Branchinecta paludosa*	*Branchinecta lindahli*	*Eubranchipus bundyi*	*Eubranchipus intricatus*	*Streptocephalus seali*	*Lynceus brachyurus*	*Lepidurus apus*	*Gammarus lacustris*	*Hyalella azecta*
	.	.	.	.	.	.	.	.	.	.	.	4	4	.	.	.	.	.	.	1	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.
	4	.	.	.	.	.	.	.	.	.	.	3	4	.	.	.	.	.	.	.	.	.	3	.	.	.	.	.	.	.	.	.	.	.	.	.
	.	.	.	.	.	.	.	.	.	.	.	.	3	.	.	.	.	.	.	.	.	.	.	.	4	.	.	.	.	.	.	.	.	.	1	.
	.	.	.	.	.	.	.	.	.	.	4	2	3	.	.	.	.	.	.	2	.	.	.	.	4	.	.	.	.	.	.	.	.	.	.	.
	.	.	.	.	.	.	.	.	.	.	3	2	2	.	.	.	.	.	.	.	.	.	.	.	4	.	.	.	.	.	.	.	.	.	.	.
	.	.	.	.	.	.	.	.	.	.	.	.	3	.	.	.	.	.	.	.	.	.	3	.	.	.	.	.	.	.	.	.	.	.	.	.
	2	.	.	.	.	.	.	.	.	.	.	.	3	.	.	.	.	.	.	.	.	.	.	.	2	.	.	.	.	.	.	.	.	.	1	.
	.	.	.	.	.	1	.	.	.	.	3	2	2	.	.	.	4	.	4	1	1	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.
	.	.	.	.	.	.	.	.	.	.	1	1	4	.	.	.	3	.	4	1	.	1	1	.	.	.	.	.	.	.	.	.	.	.	.	.
	.	.	.	.	.	.	.	.	.	.	3	3	3	3	.	.	.	.	1	.	.	.	4	.	.	.	.	.	.	.	.	.	.	.	.	.
	.	.	.	.	.	.	.	.	.	.	3	4	3	.	.	.	.	.	.	.	.	.	.	.	3	.	.	.	.	.	.	.	.	.	.	.
	.	.	.	.	.	.	.	.	.	.	.	1	4	2	.	.	.	.	.	.	.	.	2	.	4	.	.	.	.	.	.	.	.	.	.	.
	.	.	5	.	2	4	.	.	.	.	.	.	3	3	.	.	.	3	.	.	.	4	.	4	.	3	.	3	3	2	2	.	4	.	.	.
	.	.	.	.	.	.	.	.	.	.	.	1	.	3	.	.	.	.	.	2	3	.	.	.	4	.	.	.	.	.	.	.	.	.	.	.
	4?•	.	.	.	.	.	.	.	.	.	.	2	.	3	.	.	.	.	.	1	1	.	2	.	.	.	.	.	.	.	.	.	.	.	.	.
	2	.	.	.	2	.	.	.	.	.	.	4	.	4	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
	4	.	.	.	.	.	.	.	.	.	.	.	.	3	.	.	.	.	.	.	.	.	2?•	.	.	.	.	.	.	.	.	.	.	.	.	.
	.	.	.	.	.	.	3	.	.	.	.	.	.	3	.	.	.	.	.	1	3	.	.	.	3	.	.	.	.	.	.	.	.	.	1	.
?•	.	.	.	.	.	.	.	.	.	.	.	.	.	3	.	.	.	.	.	.	1	.	.	.	4	.	.	.	.	.	.	.	.	.	.	.
	.	.	.	.	.	.	.	.	.	.	.	2	.	3	.	.	.	.	.	1	.	.	.	.	4	.	.	.	.	.	.	.	.	.	.	.
	4?•	.	.	.	.	.	.	.	.	.	.	1	.	4	.	.	.	.	.	1	.	.	3	.	.	.	.	.	.	.	.	.	.	.	.	.
	3?•	.	.	.	.	.	.	1	3	.	3	4	.	3	.	.	.	.	.	1	2	.	4	.	.	.	.	.	.	.	.	.	.	.	1	.
?•	.	.	.	.	1	.	.	.	.	.	.	.	.	3	.	.	.	.	.	2	1	.	3?•	.	.	.	.	.	.	.	.	.	.	.	.	.
	.	.	.	.	2	.	3	.	.	.	.	3	.	3	.	.	.	.	.	.	1	.	3	.	1	.	.	.	.	.	.	.	.	.	.	.
	.	.	.	.	.	.	.	.	3	.	.	3	.	3	.	.	.	.	.	.	.	.	5	.	.	.	.	.	.	.	.	.	.	.	.	.
	.	.	1	.	.	.	.	.	.	.	.	.	.	2	.	.	.	.	.	3	.	.	3	.	.	.	.	.	.	.	.	.	.	.	1	1
	3	.	.	.	.	.	.	.	.	.	.	1	.	3	.	.	.	.	.	.	.	.	3	.	.	.	.	.	.	.	.	.	.	.	.	.
	3	.	.	.	.	.	.	.	.	.	1?•	1	.	3	.	.	.	.	.	.	.	.	2	.	.	.	.	.	.	.	.	.	.	.	.	.
	4	.	.	.	.	3	.	.	3	.	.	2	.	3	.	.	.	.	4	.	1	1	3	.	.	2	.	.	.	.	.	.	.	.	.	.
	.	.	.	.	.	.	.	.	3	3	.	3	.	4	.	.	.	.	4	.	.	.	3	.	.	.	.	.	.	.	.	.	.	.	.	.
	.	.	.	.	.	.	.	.	.	2	.	.	.	3	.	.	.	.	4	.	.	.	2	.	.	.	.	.	.	.	.	.	.	.	.	.
	.	.	.	.	.	.	.	.	2	.	.	.	.	2	.	3	.	.	.	.	.	.	2	.	1	.	.	.	.	.	.	.	.	.	.	.
	.	.	.	.	.	3	.	.	.	.	.	2	.	1	.	3	.	.	.	1	2	.	3	.	.	.	.	.	.	.	.	.	.	.	.	.
	4	.	.	.	.	2	.	.	.	.	.	1	.	2	.	3	.	.	.	1	1	.	3	.	.	.	.	.	.	.	.	.	.	.	.	.
	4	.	.	.	.	.	.	.	.	.	.	.	.	3	.	4	.	.	.	.	.	.	4	.	.	.	.	.	.	.	.	.	.	.	.	.
?•	.	.	.	.	1	.	.	.	.	.	.	3	.	1	.	4	.	.	.	.	1	.	3	.	.	.	.	.	.	.	.	.	.	.	.	.
	.	.	.	.	.	4	.	.	.	.	.	3	.	2	.	4	.	3	.	.	1	.	2	.	.	.	.	.	.	.	.	.	.	.	.	.
	.	.	.	.	.	.	3	.	.	.	.	2	.	2	.	.	.	4	.	.	.	1	.	.	3	.	.	.	.	.	.	.	.	.	.	1
	.	.	.	.	.	.	.	.	.	.	.	2	.	2	.	.	3	.	.	1	.	.	3	.	.	.	.	.	.	.	.	.	.	.	.	.
	3	.	.	.	.	.	.	.	.	2	2	.	.	1	.	.	4	.	.	.	.	.	2	.	.	.	.	.	.	.	.	.	.	.	.	.
	4?•	.	.	.	.	.	.	.	.	.	.	.	.	2	.	.	4	.	.	.	.	.	4?•	.	.	.	.	.	.	.	.	.	.	.	.	.
	.	.	.	.	.	.	.	.	.	.	.	3	.	4	.	.	.	.	.	2	2	.	.	.	5	.	.	.	.	.	.	.	.	.	2	.
	.	.	.	.	.	.	.	.	.	.	.	.	.	2?•	.	.	.	.	.	.	1	.	.	.	3	.	.	.	.	.	.	.	.	.	.	.
	.	.	1	.	.	.	1?•	.	.	.	.	.	.	2	.	.	.	.	.	2	2	.	2	.	4	.	.	.	.	.	.	.	.	.	.	.
	.	.	.	.	.	4	.	.	.	.	.	4	.	1	.	.	.	4	.	.	.	.	.	.	4	.	.	.	.	.	.	.	.	.	.	.
	3	.	1	.	.	.	4	.	.	.	.	.	.	2	.	.	.	4	.	3	2	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1
	4?•	.	1	.	.	3	.	.	1	.	.	.	.	3	.	.	.	5	.	3	3	.	3	.	.	.	.	.	.	.	.	.	.	.	.	.
	3?•	.	2	.	.	2	3	.	.	.	.	4	.	2	.	.	.	4	.	2	2	.	2	3	2	.	.	.	.	.	.	.	.	.	.	.
	5	.	1	.	.	.	.	.	.	.	.	.	.	3	.	.	.	.	.	.	.	.	2	.	3?•	.	.	.	.	.	.	.	.	.	.	1
	.	4	.	.	.	.	.	.	.	.	1?•	2	.	2	.	.	.	2	.	.	.	2	2	.	4	.	.	.	.	.	.	.	.	.	.	.
	.	.	.	.	.	.	.	.	.	.	3	.	.	4	.	.	.	.	.	.	1	.	4	.	.	.	.	.	.	.	.	.	.	.	.	1
	.	.	.	.	3	.	.	.	.	.	.	.	.	4	.	.	.	.	.	.	2	.	3?•	.	.	.	.	.	.	.	.	.	.	.	1	1
	2	.	.	.	1	.	.	.	.	.	.	.	.	4	.	.	.	.	.	.	.	.	3?•	.	.	.	.	.	.	.	.	.	.	.	.	.
	.	.	.	.	2	4	.	.	.	.	4	1	.	4	.	.	.	.	.	2	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
	.	.	.	.	.	4	.	.	.	.	.	4	.	.	3	.	.	4	.	.	2	.	.	.	5	.	.	.	.	.	.	.	.	.	.	.
	3	.	.	.	.	.	5	.	.	.	.	.	.	.	4	4	.	5	.	.	1	.	3	.	.	.	.	.	.	.	.	1	.	1	.	.
	3?•	.	2	1	.	3	.	.	.	1	3	3	.	.	1	.	.	2	.	2	2	.	.	.	5	.	1	.	.	.	.	.	.	.	.	1

Daphnia catawba	Simocephalus vetulus	Scapholeberis kingi	Ceriodaphnia affinis	Ceriodaphnia reticulata	Ceriodaphnia lacustris	Ceriodaphnia quadrangula	Bosmina longirostris	Macrothrix hirsuticornis	Senecella calanoides	Diaptomus franciscanus	Diaptomus tyrrelli	Diaptomus sicilis	Diaptomus ashlandi	Diaptomus nudus	Diaptomus connexus	Diaptomus oregonensis	Orthocyclops modestus	Macrocyclops ater	Macrocyclops albidus	Eucyclops agilis	Eucyclops speratus	Acanthocyclops vernalis	Diacyclops navus	Diacyclops bicuspidatus thomasi	Microcyclops varicans rubellus	Canthocamptus oregonensis	Bryocamptus zschokkei	Branchinecta paludosa	Branchinecta campestris	Eubranchipus intricatus	Streptocephalus seali	Gammarus lacustris	Hyalella azteca	Mysis relicta
.	.	.	.	.	.	.	.	.	.	.	.	.	3	.	.	.	.	.	.	.	.	1?•	.	.	.	.	.	.	.	.	.	.	.	.
.	2	.	.	.	.	.	.	.	.	.	4	.	.	.	.	.	.	.	.	2	.	.	.	.	.	.	.	.	.	.	.	.	.	.
.	.	.	.	.	.	.	.	.	.	.	3	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
.	.	.	.	.	.	.	2	.	.	.	4	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
.	.	.	4	.	.	.	2	.	.	.	3	.	.	.	.	.	.	.	.	.	.	4	.	.	.	.	.	.	.	.	.	.	.	.
.	.	.	.	.	.	.	3	.	.	.	2	.	.	.	.	.	.	.	.	.	.	.	.	2	.	.	.	.	.	.	.	.	.	.
.	.	.	.	.	.	.	4	.	.	.	2	.	.	.	.	.	.	.	.	.	.	4	.	.	.	.	.	.	.	.	.	.	.	.
.	.	.	.	.	.	.	3	.	.	.	4	.	.	.	.	.	.	.	.	.	.	3	.	.	.	.	.	.	.	.	.	.	.	.
.	.	.	1?•	.	.	.	.	.	.	.	3	.	.	.	.	.	.	.	.	.	.	2	.	.	.	.	.	.	.	.	.	.	.	.
.	.	.	.	.	.	.	2	.	.	.	3	.	.	.	.	.	.	.	.	.	.	3	.	.	.	.	.	.	.	.	.	.	.	.
3	.	.	.	.	.	.	1	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	4	.	.	.	.	.	.	.	.	.	.
.	.	.	.	.	.	.	.	.	.	.	4	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.
.	.	.	.	.	.	.	.	.	.	.	4	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
.	.	.	.	.	.	.	.	.	.	.	4	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
.	.	.	.	.	.	.	.	.	.	.	3	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
.	.	.	.	.	.	.	2	.	.	.	4	.	.	.	.	.	.	.	.	.	.	.	.	3	.	.	.	.	.	.	.	1	.	.
.	.	.	.	.	.	.	4	.	.	.	4	.	.	.	.	.	.	.	.	.	.	.	.	3	1	.	.	.	.	.	.	.	.	.
.	.	3	.	.	.	.	1	.	.	.	4	.	.	.	.	.	.	.	.	2	.	2?•	.	.	.	.	.	.	.	.	.	.	.	.
.	.	.	.	.	.	.	.	.	.	.	4	.	.	.	.	.	.	.	.	.	.	3	.	4	.	.	.	.	.	.	.	.	.	.
.	.	.	.	.	.	.	.	1	.	.	4	.	.	.	.	.	.	.	.	.	.	2	.	3	.	.	.	2	.	.	.	.	.	.
.	.	3	.	2	.	.	.	.	.	.	4	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	3	.	.	.	.	.	.
.	.	.	.	.	.	.	.	.	.	.	4	.	.	.	.	.	.	.	.	1	.	2	.	3	.	.	.	.	.	.	.	.	.	.
.	.	.	.	.	.	.	.	.	.	.	3	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
.	.	1	.	.	.	.	.	.	.	.	4	.	.	.	.	.	.	.	3	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
.	2	.	.	.	.	.	.	.	.	.	4	.	.	.	.	.	.	.	.	2	.	2	.	.	.	.	.	.	.	.	.	.	.	.
.	1	.	.	.	.	.	.	.	.	.	4	.	.	.	.	.	.	.	1	2	.	.	.	.	.	.	.	.	.	.	.	.	.	.
.	.	1	.	.	.	.	.	.	.	.	3	.	.	.	.	.	.	.	.	.	.	1	.	1	.	.	.	.	.	.	.	.	.	.
.	.	.	.	.	.	.	.	.	.	.	2	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
.	.	.	.	.	.	.	.	.	.	.	3	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.
.	.	.	.	.	.	.	.	.	.	.	4	.	.	.	.	.	.	.	.	.	.	1?•	.	.	.	.	.	.	.	.	.	.	.	.
.	.	.	.	.	.	.	.	.	.	.	.	.	2	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
.	.	.	.	4	.	.	.	.	.	.	4	.	.	.	.	.	.	.	.	.	.	3?•	.	.	.	.	.	.	.	.	.	.	.	.
.	.	.	.	.	.	.	.	.	.	.	4	.	.	.	.	.	.	.	.	.	.	2	.	.	.	2?•	.	.	.	1	2	.	.	.
.	2	1	.	4	.	.	.	.	.	.	4	.	.	3	.	.	.	.	.	.	.	2	.	.	.	1	.	.	.	.	.	.	.	.
.	.	.	.	.	.	.	1	.	1	.	.	4	.	.	.	.	.	.	.	.	.	.	.	4	.	.	1?•	.	.	.	.	.	.	1
.	.	.	.	.	.	.	3	.	1	.	.	4	.	.	.	.	.	.	.	.	.	1	.	3	.	.	.	.	.	.	.	.	.	.
.	.	.	.	.	.	.	1	.	.	.	.	4	.	.	.	.	.	.	1	1	.	1	.	3	.	.	.	.	.	.	.	.	.	.
2?•	.	.	3	.	2	.	3	.	.	.	.	4	.	.	.	.	4	.	.	.	.	3	.	.	.	.	.	.	.	.	.	.	.	.
2	.	.	.	.	.	.	2	.	.	.	.	4	.	.	.	.	.	.	1	1	1	.	.	4	.	1	.	1?•	.	.	.	.	.	.
.	.	.	.	.	2	4	3	.	.	.	.	4	.	.	.	.	.	.	1	1	.	2	.	4	.	.	.	.	.	.	.	1	.	.
.	.	.	.	.	.	.	3	.	.	.	.	4	.	.	.	.	.	.	.	.	.	.	.	5	.	.	.	.	.	.	.	.	.	.
.	.	.	2	.	.	.	2	.	.	.	.	4	.	.	.	.	.	.	.	2	.	4	.	.	1	.	.	.	.	.	.	.	.	.
1?•	.	1	.	.	.	.	4	.	.	.	.	4	.	.	.	.	.	.	.	1	.	4	.	1	.	.	.	.	.	.	.	.	.	.
.	.	.	.	.	.	.	.	.	.	.	.	4	.	.	.	.	.	.	.	.	.	3	.	.	.	.	.	.	.	.	.	.	.	.
.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.	1	.	1	.	.	.	1?•	.	.	.	.	.	.	.	.
.	3	.	3	3	.	.	.	.	.	.	.	.	.	3	.	.	.	.	.	.	.	4	3	.	.	.	.	3	.	.	.	.	.	.
.	.	.	.	.	.	.	4	.	.	.	.	.	.	3	.	.	.	.	.	.	.	1	.	4	.	.	.	.	.	.	.	.	.	.
.	1	.	.	.	.	.	4	.	.	.	.	.	.	3	.	.	.	1	.	.	.	.	.	4	.	.	.	.	.	.	.	.	.	.
.	.	.	.	.	.	.	4	.	.	.	.	.	.	4	.	.	.	.	1	.	.	.	.	4	.	.	.	.	.	.	.	.	.	.
.	.	.	.	.	.	.	3	.	.	.	.	.	.	3	.	.	.	.	1	2	.	.	.	4	.	.	.	.	.	.	.	2	.	.
.	.	.	.	.	.	.	.	.	.	.	.	.	.	4	.	.	.	.	1	.	.	3	.	1?•	.	.	.	.	.	.	.	2	.	.
.	.	.	1?•	.	.	.	.	.	.	.	.	.	.	3?•	.	.	.	.	.	.	.	1	.	3	.	.	.	.	.	.	.	.	.	.
.	1	.	.	.	.	.	.	.	.	.	.	.	.	4	.	.	.	.	1?•	.	.	1?•	.	.	.	.	.	.	.	.	.	.	.	.
.	.	.	.	.	.	.	.	.	.	4	.	.	.	.	.	.	.	.	.	.	.	2?•	.	.	.	.	.	.	.	.	.	.	.	.
.	.	.	.	.	.	.	3	.	.	.	.	.	.	.	.	4	.	.	.	.	.	.	.	4	.	.	.	.	.	.	.	.	.	.
.	.	.	.	.	.	.	.	.	.	.	.	.	.	3	.	.	.	.	.	.	.	2?•	.	.	.	.	.	.	.	.	.	.	1	.
.	.	.	.	.	.	.	3	.	.	.	.	.	.	2	.	.	.	.	1	.	.	.	.	5	.	.	.	.	.	.	.	.	.	.
.	.	1	.	.	.	1	.	.	.	.	.	1?•	.	.	.	.	.	.	.	.	.	.	3	.	.	.	.	.	.	.	.	.	.	.
.	.	2	.	.	.	2	.	.	.	.	.	4	.	.	.	.	.	.	.	.	.	.	3	.	.	.	.	.	.	.	.	.	.	.
.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	5	.	.	.	.	.	.	.	.	.	.	.	.	.	3	.	.	.	.	.
.	.	2	.	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.	4	.	.	.	.	.	.	.	.	.	.

Lake No.	Name	Reference	Date for chem data	Elevation (*m*)	Area (*ha*)	Max known depth (*m*)	Secchi disc depth (*m*) max known	pH
J 571	Harvey L.	11U/MJ030904	12.9.68	1617	37.0	20.0	5.0	8.1
J 273	Rosemarie P.	11U/MJ570434	21.8.69	1714	0.4	2.3	+[d]	8.2
J 271	Moose P.	11U/MJ572427	21.8.69	1707	0.2	0.5	+[d]	8.7
J 294	Leach P. #1	11U/MJ393372	18.6.70	1223	2.5	1.5	+[d]	8.5
J 295	Leach L.	11U/MJ390384	18.6.70	1226	8.5	11.0	9.2	8.3
J 802	S. Salt Lick P.	11U/MJ352921	29.8.69	1000	<0.1	2.0	+[d]	8.3
J 801	N. Salt Lick P.	11U/MJ352922	29.8.69	1000	<0.1	2.0	+[d]	8.3
J 506	N. Cold Sulfur P.	11U/MJ278777	29.8.69	1006	3.5	2.5	+[d]	8.2
J 384	Edith P.	11U/MJ313630	19.5.70	1038	2.3	1.3	–	8.0
J 368	Beaver L.	11U/MJ513573	15.7.70	1498	29.0	1.5	+[d]	8.8
J 393	Lac Beauvert	11U/MJ286594	6.4.70	1030	33.0	21.0	19	8.2
B 192	Hidden L.	11U/NH620039	20.8.66	2278	11.0	32.3	11.4	7.9
B 199	Little Baker L.	11U/NH675039	19.8.66	2240	2.0	5.0	+[d]	8.4
B 201	Tilted L.	11U/NH679038	19.8.66	2200	3.0	8.0	8.0	8.0
B 97	Up. Consolation L.	11U/NG594843	20.9.67	1958	9.7	9.7	9.0	8.2
B 85	West Altrude L.	11U/NG667757	24.6.70	1628	3.0	6.1	+[d]	8.5
B 83	Vista L.	11U/NG681764	25.6.70	1567	8.0	6.5	+[d]	8.4
B 457	Warden L.	11U/NH213584	13.7.70	1400	6.0	2.2	+[d]	8.7
B 242	Snowflake L.	11U/NH808167	21.8.67	2320	7.1	13.0	9.0	8.1
B 240	Grouse L.	11U/NH848168	23.8.72	2271	10.0	9.0	5.0	8.2
B 501	N. Cuthead P.	11U/NH867004	24.8.68	2210	0.3	1.3	0.5	8.4
B 227	Cuthead L.	11U/NH867003	22.8.72	2210	3.5	4.3	+[d]	8.2
Y 41	Celeste L.	11U/NH337074	10.8.72	1997	2.0	5.7	+[d]	8.1
Y 42	Duchesnay L.	11U/NH347080	12.8.70	1595	3.5	1.0	+[d]	9.9
Y 49	Summit L.	11U/NG492999	7.7.70	1628	2.0	1.3	+[d]	9.0
Y 48	Sink L.	11U/NG482998	5.8.71	1622	5.0	2.0	+[d]	8.2
Y 26	Emerald L.	11U/NG327990	5.7.66	1300	116.0	28.1	3.1	8.1
Y 7	Schaffer L.	11U/NG454885	6.8.66	2170	0.4	2.5	+[d]	8.0
BC	Grizzly L.	11U/NG846568	25.8.66	2200	3.6	3.0	+[d]	8.4
BC	Rock Isle L.	11U/NG853573	25.8.66	2272	5.0	12.5	8.5	8.3
BC	Upper Elk L.	11U/PG340015	16.8.70	1747	65.0	30.0	2.5	–
A	Nutcracker P.	11U/PF858626	7.8.67	1881	0.5	0.8	+[d]	7.3
A	Tadpole P.	11U/PF833657	7.8.67	1798	<0.1	0.5	+[d]	7.8
W 48A	Indian springs P.	12U/TK901454	11.8.71	1351	2.5	2.0	+[d]	8.6
W 17	Up. Waterton L.	12U/TK880350	25.8.72	1278	960.0	135.5	10.0	8.0
W 19	Lo. Waterton L.	12U/TK900370	25.8.72	1278	470.0	25.6	9.5	8.1
W 22	Knights L.	12U/TK918413	24.8.72	1277	145.0	7.3	+[d]	8.1
J 419	Iris L.	11U/MJ178591	17.7.70	1302	6.0	12.5	8.0	8.5
J 396	Pyramid L.	11U/MJ262640	20.8.72	1186	120.0	19.0	6.0	8.0
J 397	Patricia L.	11U/MJ259618	8.66	1180	69.0	42.0	14.5	8.6
J 385	Edith L.	11U/MJ300625	20.8.72	1024	50.0	19.0	13.0	8.3
J 328	1st of five L.	11U/MJ313528	14.7.70	1110	14.0	22.0	11.5	8.5
J 287	Horseshoe L.	11U/MJ417389	20.8.72	1230	13.0	23.0	12.0	8.0
J 221	Maligne L.	11U/MJ588400	10.7.66	1675	3940.0	96.0	6.5	7.9
B 419	Up. Waterfowl L.	11U/NH266422	14.6.66	1670	48.0	4.7	0.7	8.1
B 504	Snowflake P.	11U/NH817176	7.70	2299	0.1	0.7	–	–
B 64	Vermilion #1	11U/NG983706	13.6.69	1384	20.0	3.0	+[d]	8.3
B 62	Vermilion #2	11U/NG976704	13.6.69	1384	18.0	2.0	+[d]	8.3
B 61	Vermilion #3	11U/NG958699	13.6.69	1387	11.0	4.0	+[d]	8.1
J 505	Edna L.	11U/MJ305808	29.8.69	1000	25.0	2.0	+[d]	8.2
J 506A	So. cold sulfur P.	11U/MJ273773	29.8.69	1006	0.4	1.5	+[d]	8.5
J 386	Ochre P.	11U/MJ300618	19.5.70	1024	0.6	0.5	+[d]	8.8
A	Evans-Thomas P.	11U/PG302371	8.69	1532	4.0	3.0	–	–
A	N. Cougar P.	11U/PG447145	7.65	2081	2.0	2.0	–	–
A	Chiniki L.	11U/PG452627	20.6.71	1337	130.0	12.0	–	8.4
W 20	Pond 20	12U/TK886363	19.7.71	1336	0.8	1.0	+[d]	8.5
W 33	Beaver P. 33	12U/UK005370	7.6.71	1524	5.5	1.5	+[d]	8.3
P	K-4	12U/UM404758	21.5.69	915	<0.1	1.0	–	–
P	K-3	12U/UM401758	21.5.69	915	<0.1	0.5	–	–
P	Gooseberry L.	12U/WN180740	3.7.63	695	430	3.0	–	11.0
A	S. Hogarth	11U/PG185280	3.7.65	1915	2.7	6.0	–	7.2

---

[e] Na > Mg as dominant cations in this lake.
[f] Other footnotes as in Table 2 and 4.

Table 6. Crustacean plankton density, species composition and abundance, and some limnological features for 62 Group V lakes and ponds.[a]

TDS (*ppm*)	Heat content (*Kcal*)	Crustacean plankton				*Lepodora kindtii*	*Polyphemus pediculus*	*Sida crystallina*	*Diaphanosoma brachyurum*	*Diaphanosoma leuchtenbergianum*	*Eurycercus lamellatus*	*Acroperus harpae*	*Graptoleberis testudinaria*	*Leydigia quadrangularis*	*Alona guttata*	*Alona affinis*	*Alona costata*	*Alona rectangula*	*Alonella nana*	*Alonella excisa*	*Chydorus sphaericus*	*Chydorus ovalis*	*Pleuroxus striatus*	*Pleuroxus procurvus*	*Daphnia rosea*	*Daphnia galeata mendotae*	*Daphnia middendorffiana*	*Daphnia pulex*	*Daphnia pulicaria*	*Daphnia schoedleri*
		Max no. per liter	Total no. spp.	Cladocera spp.	Copepoda pp.																									
91	8.2	5.4	2	0	2	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
345	7.6	25.0	4	2	2	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	3	.	.
82	16.4	20.0	2	1	1	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
104	23.0^{b}	95.0	4	3	1	.	3	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	4
141	17.1	64.7	7	5	2	.	.	.	.	3	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.	.	3
209	14.6	6.5	9	7	2	.	.	1	.	.	.	.	.	.	2	.	.	.	1	1	.	1	.	.	.	.	.	.	.	1?^{e}
209	14.6	10.0	6	4	2	.	.	1	.	.	.	.	.	.	.	.	.	.	1	.	.	1	.	.	.	.	.	.	.	.
513	13.3	30.0	5	3	2	.	2	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.
188	14.0	25.0	8	6	2	.	.	.	.	.	.	1	.	.	.	1	.	.	.	.	1	.	.	.	4	.	.	.	2	.
124	17.6	18.2	5	3	2	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.	4	.	.
135	10.1	51.0	8	6	2	.	.	.	.	.	1	.	.	.	.	.	.	.	1	.	1	.	.	.	3	.	.	.	.	.
71	7.8	21.9	3	1	2	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.
60	7.3	30.0	2	1	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.
60	9.1	25.0	2	1	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.
59	4.8	1.5	2	1	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.
150	17.0	20.0	7	4	2	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	1	.	.	.	.	.	.	4	.	.
130	13.9	30.0	5	2	3	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	3	.	.	.	.
109	15.9	20.0	8	5	3	.	.	.	.	.	.	.	.	.	.	2	.	.	1	.	2	.	.	.	.	.	.	.	.	.
102	8.5	85.0	7	4	3	.	.	.	.	.	.	1	.	.	1	.	.	.	.	.	2	.	.	.	.	.	.	1	.	.
86	9.3	81.1	9	5	3	.	.	.	.	.	.	.	.	.	.	.	.	1?^{e}	.	.	2	.	.	.	.	.	2	3	.	.
90	9.0^{b}	60.0	4	2	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
83	7.7	27.5	6	2	4	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	2	.	.	.
72	14.5	11.1	2	1	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	3?^{e}	.	.
57	18.2	45.0	5	3	2	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	3	.	.	.	.	.	.	4	.	.
90	22.8	23.3	10	7	3	.	2	.	.	.	1	1	.	.	.	.	.	.	.	2	2	.	.	.	.	.	.	4	.	.
109	18.2	142.4	8	5	3	.	2	.	.	.	1	.	.	.	.	.	.	.	.	.	2	.	.	.	.	.	.	.	4?^{e}	.
122	7.9	9.0	4	1	3	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
55	7.3	0.6	1	0	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
100	17.9	15.0	2	0	2	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
83	11.7	25.0	3	1	2	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.
–	–	0.4	1	0	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
27	27.3	80.0	5	3	2	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	2	.	.	.	.	.	.	3	.	.
13	23.6	35.0	6	1	3	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	4	.	.
188^{f}	24.6	100.0	12	8	4	.	.	.	.	.	.	.	.	.	1	.	.	.	3	1	2	.	.	.	.	.	.	.	.	2?^{e}
62	12.9	77.7	12	7	4	.	1	.	.	.	.	1	.	.	1	1	.	.	.	.	1	.	.	.	3?^{e}	.	.	.	.	.
67	11.4	44.8	8	4	4	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	1	.	.	.	4?^{e}	.	.	.	.	.
75	14.5	32.6	7	2	5	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.
139	12.5	60.4	8	5	3	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	3	.	.	.	.	.
122	11.2	66.6	16	10	6	1	.	1	.	3	.	1	1	.	.	.	.	.	.	.	1	.	.	.	.	3	.	2	.	.
358^{f}	11.7	58.0	22	16	5	1	1	.	.	2	1	1	.	1	1	1	.	1	1	.	1	.	.	.	.	1	.	3	.	.
161	17.7	174.0	8	6	2	1	.	.	.	.	.	.	.	.	.	1	.	.	.	.	1	.	.	.	3	.	.	.	.	2
168^{e}	16.8	73.5	9	5	4	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	3	.	.	.	.	2?^{e}
112	10.0	68.3	10	6	4	.	2	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	.	4	.	.	.	.	.
101	11.3	25.6	5	3	2	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.	3	.	.
95	6.8	0.3	5	1	4	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.
75	9.3	70.0	9	5	3	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	3	.	.	.	.	.	.	4	.	.
133	19.4	120.0	10	7	3	.	2	.	2	.	.	.	.	.	.	1	.	.	1	.	2	.	.	.	5	.	.	.	.	.
169	18.2	140.0	11	8	3	.	2	.	3	.	.	.	.	.	.	1	.	.	2	.	2	.	.	.	4	.	.	.	.	.
118	18.0	95.0	10	7	3	.	.	.	.	.	.	.	.	.	.	1	.	.	1	.	1	.	1	1	4	.	.	.	.	.
285	11.4	55.0	14	9	4	.	1	.	.	.	.	.	.	.	1	1	1	.	.	1	2	1	.	.	.	.	.	.	.	4
372	13.3	65.0	7	2	4	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.	4	.
182	22.0	7.7	5	2	3	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	2	.	.	.	.	.	.	.	.	.
–	18.0^{b}	85.0^{b}	7	4	3	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	2	.	.	.	.	.	.	1	.	.
–	17.0^{b}	30.0	4	2	2	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	2	.	.	.	.	.	3	.	.	.
172	16.8	120.0^{b}	4	2	2	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	2?^{e}	.	.	.	.
145	26.4	50.0	6	3	2	.	3	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.	3?^{e}	.
166	16.3	452.0	4	1	3	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
–	30.0^{b}	90.0^{b}	5	3	2	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	4	.	.
–	30.0^{b}	150.0^{b}	6	4	2	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	3	.	.	.	.	.	.	4	.	.
$29{,}800^{ef}$	26.0^{b}	150.0	2	0	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
115	18.0^{b}	45.0	4	2	2	.	3	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.

Lake No.	Name	Grid reference
J 539	Mahood L.	11U/LJ956757
J 481	Henry L.	11U/MJ152666
J 490	Zengel P.	11U/MJ218702
J 387	Annette L.	11U/MJ296616
J 389	Trefoil #2	11U/MJ293605
J 371	Jacques L.	11U/MJ498644
J 377	Tekarra L.	11U/MJ360557
J 333	Wabasso L.	11U/MJ337488
J 146	Osprey L.	11U/MJ547232
J 197	Lo. Geraldine L.	11U/MJ371298
J 182	Chalk L.	11U/MJ152200
J 91	Wolverine L.	11U/MJ830155
B 283	Helen L.	11U/NH406260
B 172	L. Louise	11U/NG540958
B 166	McNair P.	11U/NG587952
B 241	Harrison L.	11U/NH825119
B 228	Wigmore P.	11U/NH900048
B 233	Bighorn L.	11U/NH939021
B 502	S. Cuthead P.	11U/NH868003
B 505	Gravel Pit	11U/PG040778
B 72	L. Minnewanka	11U/PG059785
B 74	Two Jack L.	11U/PG052762
Y 43	Yoho L.	11U/NH359024
Y 44	Hidden L.	11U/NH360035
Y 47	Sherbrooke L.	11U/NH427005
Y 17	Ross L.	11U/NG486984
Y 19	N. Narao L.	11U/NG455971
Y 18	S. Narao L.	11U/NG455967
Y 10	Mary L.	11U/NG465888
Y 13	Opabin #3	11U/NG474881
Y 11	Opabin #4	11U/NG473883
K 1	Olive L.	11U/NG753139
G 10	Marion L.	11U/MG646787
R 7	Up. Jade L.	11U/MG247580
R 8	Lo. Jade L.	11U/MG252586
R 4	Eva L.	11U/MG225953
R 5	Millar L.	11U/MG227581
R 3	Heather P.	11U/MG201556
R 1	E. Balsam P.	11U/MG196548
R 2	W. Balsam P.	11U/MG192548
W 11	Up. Carthew L.	12U/TK811344
W 12	Lo. Carthew L.	12U/TK814347
W 15	Crandell L.	12U/TK834411
W 16	Bertha L.	12U/TK850341
W 54	Lone L.	11U/QE095411
W 57	Peck's Basin	11U/QE082447
W 59	Up. Twin L.	11U/QE074461
W 53	Goat L.	11U/QE122494
W 39	Giant's Mirror	12U/UK038366
W 9	Summit L.	11U/QE177324
J 471	Moren #1	11U/LJ964747
J 444	Rink L.	11U/LJ932624
J 481B	E. Henry P.	11U/LJ150658

---

*Footnotes as in Table 2.

TABLE 7. Crustacean plankton density, species composition and abundance, and some limnological features for 53 Group VI lakes and ponds.[a]

Date for chem data	Elevation (*m*)	Area (*ha*)	Max depth (*m*) max found	Secchi disc depth (*m*) max found	pH	TDS (*ppm*)	Heat content (*kcal*)	Crustacean Plankton				*Polyphemus pediculus*	*Sida crystallina*	*Holopedium gibberum*	*Alona guttata*	*Alona affinis*	*Alona costata*	*Alona rectangula*	*Alona intermedia*	*Chydorus sphaericus*	*Daphnia rosea*	*Daphnia galeata mendotae*	*Daphnia middendorffiana*	*Daphnia pulex*	*Daphnia schoedleri*
								Max No. per liter	Total No. spp.	Cladocera spp.	Copepoda spp.														
19.8.70	1995	48.0	28.0	9.0	7.3	14^{c}	7.8	7.1	5	4	1	.	.	3	1	.	.	.	.	1	.	.	.	.	.
12.9.68	1950	10.0	11.7	10.5	7.2	11^{c}	7.0^{b}	0.1	1	0	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.
12.9.68	2148	2.0	1.2	+^{d}	8.4	90^{c}	8.0^{b}	3.1	1	0	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.
16.6.70	1024	28.0	22.0	16.0	8.4	153	19.0^{b}	66.1	6	5	1	1	.	.	.	.	.	.	.	1	4	.	.	.	.
19.5.70	1030	1.8	17.0	10.0	8.3	134	17.0^{b}	26.9	6	5	1	.	.	.	.	.	.	.	.	2	.	3	.	.	.
15.7.70	1517	27.0	4.5	+^{d}	8.3	155^{c}	12.7	14.1	6	4	2	.	.	.	.	.	.	.	.	2	.	.	3	2?^{e}	.
11.9.68	2233	2.0	7.0	2.5	8.3	9	4.5	2.7	2	1	1	.	.	.	.	.	.	.	.	.	.	.	.	3	.
18.7.70	1143	3.5	2.0	1.0	8.0	88	12.8	1.1	2	1	1	.	.	.	.	.	.	.	.	2	.	.	.	.	.
13.7.70	1387	5.4	7.4	1.5	8.4	37	16.2	5.2	3	2	1	.	.	.	2	.	.	.	.	2	.	.	.	.	.
14.7.70	1600	16.0	6.0	+^{d}	8.0	53	10.5	0.3	2	1	1	.	.	.	.	.	.	.	.	1	.	.	.	.	.
28.8.69	2210	12.0	32.0	1.5	7.7	3	6.5	1.3	1	0	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.
7.9.67	2250	1.5	2.0	5.0	8.1	75	12.0^{b}	0.2	2	1	1	.	.	.	.	.	.	.	.	1	.	.	.	.	.
29.7.66	2347	2.6	12.0	5.7	7.6	54	5.1	0.4	2	1	1	.	.	.	.	.	.	.	.	.	.	.	1	.	.
23.6.66	1732	78.0	69.0	2.5	8.6	75	6.4	0.7	2	1	1	.	.	.	.	.	.	.	.	.	.	.	.	1	.
9.11.71	1534	1.4	3.5	+^{d}	8.4	123	19.0^{b}	10.0	4	3	1	.	.	.	.	.	.	.	.	1	2	.	.	.	.
22.8.72	2243	8.4	10.7	4.5	8.1	135	8.4	207.0	3	1	2	.	.	.	.	.	.	.	.	.	.	.	.	3	.
4.6.70	1996	2.0	0.9	+^{d}	8.2	129	18.2	12.0	4	3	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.
22.8.72	2347	2.2	9.2	6.5	8.2	86	7.5	5.3	1	0	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.
24.8.68	2210	0.2	0.5	+^{d}	8.4	85	9.0^{b}	50.0	4	2	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.
9.7.68	1457	0.3	5.0	+^{d}	–	–	8.9	0.1	1	0	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.
7.7.70	1480	1663.0	105.0	10.4	8.3	165	9.8	25.0	7	5	2	.	.	.	.	.	.	.	.	1	2	3?^{e}	.	.	.
23.6.70	1476	35.0	16.0	9.4	8.4	168	12.1	30.0	8	6	2	.	.	.	.	.	2	.	.	1	3	3?^{e}	.	.	.
12.8.70	1825	3.3	12.0	+^{d}	8.4	121	14.5	6.2	1	0	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.
12.8.70	1845	0.5	8.0	5.0	8.4	127	15.0	47.2	2	1	1	.	.	.	.	.	.	.	.	1	.	.	.	.	.
5.8.66	1800	35.0	12.0	2.0	7.9	78	9.7	2.0	3	1	2	.	.	.	.	.	.	1	.	.	.	.	.	.	.
7.7.70	1729	6.0	21.5	12.5	8.3	109	15.8	9.2	3	2	1	.	.	.	.	.	.	.	.	1	.	.	.	.	.
9.7.70	1715	3.0	1.2	+^{d}	8.3	86	17.3	0.7	7	5	2	1	2	.	.	2	.	.	.	1	.	.	.	.	.
9.7.70	1715	0.7	6.3	+^{d}	8.4	113	15.3	48.1	7	4	3	2	3	.	.	.	.	.	.	.	.	.	.	.	.
8.7.70	2034	6.5	3.5	+^{d}	8.8	51	12.3	21.0	4	2	2	.	.	.	.	.	.	.	.	2	.	.	.	.	.
31.7.68	2234	0.3	1.5	+^{d}	8.1	10	12.8	50.0	2	1	1	.	.	.	.	.	.	.	.	2	.	.	.	.	.
31.7.68	2234	0.3	1.4	+^{d}	8.1	10	16.0	80.0	3	2	1	.	.	4	.	.	.	.	.	2	.	.	.	.	.
9.8.72	1631	0.8	3.2	+^{d}	7.8	176	10.7	190.0	2	1	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.
23.6.70	1723	0.5	6.0	+^{d}	6.0	3^{c}	10.5	10.0	4	3	1	.	.	.	.	.	.	.	.	2	.	.	.	3	.
10.8.70	1814	7.5	13.0	13.0	6.8	12^{c}	9.0	5.1	3	1	2	.	.	3	.	.	.	.	.	.	.	.	.	.	.
10.8.70	1762	4.0	22.5	17.5	6.8	9^{c}	7.9	26.3	4	2	2	.	.	3	1	.	.	.	.	.	.	.	.	.	.
29.6.70	1927	3.2	12.0	10.0	7.3	4	13.2	39.0	2	1	1	.	.	4	.	.	.	.	.	.	.	.	.	.	.
29.6.70	1899	8.5	27.0	18.5	7.3	10	8.4	9.2	3	1	2	.	.	3	.	.	.	.	.	.	.	.	.	.	.
29.6.70	1927	0.2	1.5	+^{d}	7.3	5	13.9	0.9	4	3	1	.	.	2	.	.	.	.	.	1	.	.	.	1	.
29.6.70	1845	0.5	1.8	+^{d}	7.3	8	14.2	48.2	3	2	1	.	.	.	.	.	.	.	.	1	.	.	.	3	.
29.6.70	1845	0.3	1.2	+^{d}	7.4	2	12.9	14.2	4	3	1	.	.	2	.	.	.	.	.	2	.	.	.	4	.
16.8.71	2195	4.5	12.0	5.0	8.0	30	8.4	155.7	3	2	1	.	.	.	.	.	.	.	.	2	.	.	.	.	5
26.8.70	2159	6.0	12.0	+^{d}	8.3	45	11.7	40.6	9	7	2	.	.	.	.	.	.	1	1	2	1?^{e}	3	.	.	4
23.7.70	1524	6.0	15.0	10.0	8.4	113	6.7	204.5	5	4	1	.	.	.	.	.	.	.	.	.	2?^{e}	4	.	.	.
26.8.70	1774	28.0	50.3	17.5	8.1	48	8.8	108.9	4	3	1	.	.	.	.	.	.	.	.	.	3	.	.	.	2
23.7.71	2027	2.5	13.0	6.5	7.1	15	7.8	49.2	3	2	1	.	.	1	.	.	.	.	.	.	2	.	.	.	.
3.10.67	1951	1.0	1.5	+^{d}	8.2	36	7.8	0.4	2	1	1	.	.	.	.	.	.	.	.	1	.	.	.	.	.
3.6.71	1963	6.0	13.5	11.0	8.2	30	10.5	89.8	4	3	1	.	.	3	.	.	.	.	.	.	.	3?^{e}	.	.	.
23.7.70	1982	2.5	8.5	8.0	8.3	46	8.5^{b}	16.2	1	0	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.
7.06.71	1384	0.5	5.0	+^{d}	8.0	322	8.2	366.5	14	7	5	.	.	.	1	2	.	.	.	1	2	.	.	.	.
25.8.70	1931	1.8	2.0	+^{d}	7.0	4	19.1	24.4	4	3	1	.	.	4	.	.	.	.	.	1	.	.	.	3	.
19.8.70	2073	3.0	10.0	9.5	7.7	3	10.8	15.5	2	1	1	.	.	4	.	.	.	.	.	.	.	.	.	.	.
19.8.70	1793	15.0	6.0	6.0	7.4	12	9.7	6.0	2	1	1	.	.	3	.	.	.	.	.	.	.	.	.	.	.
12.9.68	2105	3.5	4.5	+^{d}	7.2	7^{c}	5.9	0.7	3	2	1	.	.	.	.	.	.	.	.	1	.	.	1?^{e}	.	.

Daphnia catawba	*Simocephalus vetulus*	*Scapholeberis kingi*	*Ceriodaphnia affinis*	*Ceriodaphnia reticulata*	*Ceriodaphnia pulchella*	*Bosmina longirostris*	*Diaptomus arcticus*	*Orthocyclops modestus*	*Macrocyclops albidus*	*Eucyclops agilis*	*Acanthocyclops vernalis*	*Diacyclops bicuspidatus thomasi*	*Canthocamptus oregonensis*	*Branchinecta paludosa*	*Gammarus lacustris*	*Hyalella azteca*
3 ?•	.	.	.	.	.	.	.	.	.	.	3	.	.	.	.	.
.	.	.	.	.	.	.	.	.	.	.	1 ?•	.	.	.	.	.
.	.	.	.	.	.	.	.	.	.	.	.	3 ?•	.	.	.	.
3	.	.	.	.	.	1	.	.	.	.	.	4	.	.	.	.
3	.	.	.	.	1	1	.	.	.	.	.	4	.	.	.	.
.	1	.	.	.	.	.	.	.	.	.	2	4	.	.	.	.
.	.	.	.	.	.	.	.	.	.	.	.	2 ?•	.	.	.	.
.	.	.	.	.	.	.	.	.	.	.	.	2	.	.	.	.
.	.	.	.	.	.	.	.	.	.	.	3	.	.	.	.	.
.	.	.	.	.	.	.	.	.	.	.	2	.	.	.	.	.
.	.	.	.	.	.	.	.	.	.	.	3	.	.	.	.	.
.	.	.	.	.	.	.	.	.	.	.	2	.	.	.	.	.
.	.	.	.	.	.	.	.	.	.	.	2	.	.	.	.	.
.	.	.	.	.	.	.	.	.	.	.	2	.	.	.	.	.
.	.	.	.	.	.	2	.	.	.	.	.	3	.	.	.	.
.	.	.	.	.	.	.	.	.	1	.	.	5	.	.	.	.
.	1	.	.	2 ?•	.	2	.	.	.	.	3	.	.	.	.	.
.	.	.	.	.	.	.	.	.	.	.	.	3 ?•	.	.	.	.
.	.	4	.	3	.	.	.	.	.	.	.	3	.	3	.	.
.	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.
3	.	.	.	.	.	4	1	.	.	.	.	4	.	.	.	.
3	.	.	.	.	.	3	1 ?•	.	.	.	.	4	.	.	.	.
.	.	.	.	.	.	.	.	.	.	.	3	.	.	.	.	.
.	.	.	.	.	.	.	.	.	.	.	4	.	.	.	.	.
.	.	.	.	.	.	.	.	.	1	.	3	.	.	.	.	.
.	.	.	.	.	.	3	.	.	.	.	3	.	.	.	.	.
.	.	.	1	.	.	.	.	.	.	2	2	.	.	.	.	.
.	.	3	4	.	.	.	.	.	1	2	4	.	.	.	.	.
4 ?•	.	.	.	.	.	.	.	1	.	1	.	.	.	.	.	.
.	.	.	.	.	.	.	.	.	.	.	4	.	.	.	.	.
.	.	.	.	.	.	.	.	.	.	.	4	.	.	.	.	.
.	.	2	.	.	.	.	.	.	.	.	.	4	.	.	.	.
.	2	.	.	.	.	.	.	.	.	.	2	.	.	.	.	.
.	.	.	.	.	.	.	.	1	.	.	3	.	.	.	.	.
.	.	.	.	.	.	.	.	3	.	.	1	.	.	.	.	.
.	.	.	.	.	.	.	.	.	.	.	3	.	.	.	.	.
.	.	.	.	.	.	.	.	2	.	.	1	.	.	.	.	.
.	.	.	.	.	.	.	.	.	.	.	2	.	.	.	.	.
.	.	.	.	.	.	.	.	.	.	.	4	.	.	.	.	.
.	.	.	.	.	.	.	.	.	.	.	3	.	.	.	.	.
.	.	.	.	.	.	.	.	.	.	.	3	.	.	.	.	.
.	.	.	.	.	.	4	.	.	.	1	3	.	.	.	.	.
.	.	.	2	.	.	5	.	.	.	.	.	4	.	.	.	.
.	.	.	.	.	.	4	.	.	.	.	4	.	.	.	.	.
.	.	.	.	.	.	.	.	.	.	.	4	.	.	.	.	.
.	.	.	.	.	.	.	.	.	.	.	2	.	.	.	.	.
.	.	.	.	.	.	3	.	.	.	.	.	4	.	.	.	.
.	.	.	.	.	.	.	.	.	.	.	.	4	.	.	.	.
.	3	2	2	.	.	.	.	.	1	1	2	5	1	.	1	1
.	.	.	.	.	.	.	.	.	.	.	1 ?•	.	.	.	.	.
.	.	.	.	.	.	.	.	.	.	.	3	.	.	.	.	.
.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.
.	.	.	.	.	.	.	.	.	.	.	2	.	.	.	.	.

12

and cold lakes. It occurred in 13 waters, all in the Bow River drainage. These occurrences and six reported by Mayhood et al. (1973) indicate that this species may be more widespread in western Canada than once supposed (Carl 1940; Wilson 1958).

D. ashlandi is usually considered a species characteristic of deep, oligotrophic lakes (Carl 1940; Patalas and Salki 1973; Whittaker and Fairbanks 1958). In this study, it occurred only in three fairly large, cold, low-salinity (TDS = 91–127 ppm) lakes.

Diaptomus nevadensis, *Branchinecta gigas*, *B. mackini*, and *Daphnia similis* appear to be restricted to high-salinity waters and were found only in the saline-soils belt of the prairie region. These four species frequently occur together in saline prairie lakes, often with *Diaptomus sicilis*. A salt concentration of about 16,000 ppm has sometimes been considered the upper limit for "freshwater" calanoid copepod species (Patalas 1964; Whittaker and Fairbanks 1958). *Diaptomus connexus* also may be confined to high-salinity waters (Anderson 1970d); in this study it occurred at a salinity of 29,800 ppm. What was probably the same species (reported as *D. siciloides*) was reported in a Saskatchewan lake reaching a salinity of 120,000 ppm (Rawson and Moore 1944). *Diaptomus nevadensis* occurred at salinities from 1121 to 6213 ppm, but is known to occur in Seagrams Lake in west-central Saskatchewan at a salinity of 19,500 ppm (G. Fabris and R. Hartland-Rowe personal communication).

Diaptomus sicilis has been variously reported as a coldwater or winter form in lakes (Rigler and Langford 1967; Carter 1971; Patalas 1971), a temporary pool and stagnant lake form (Carl 1940), or a species adapted to a wide range of habitats (Reed 1959; Whittaker and Fairbanks 1958). In this study, it occurred at salinities from 62 to 6213 ppm, in permanent mountain lakes and shallow, saline prairie lakes, and was capable of tolerating a wide range of temperature conditions. The upper limit of salinity tolerance is undoubtedly much higher than found here. Although Whittaker and Fairbanks (1958) did not report copepods from Soap Lake, Washington State (up to 38,700 ppm), I have identified both *D. sicilis* and *D. connexus* from this lake. Bajkov (1929) reported *D. sicilis* as a high-altitude form in Jasper National Park and *D. tyrrelli* as characteristic of lakes at lower altitudes in the park, whereas in fact the present broader study has shown the reverse to be true. In cold waters, *D. sicilis* develops slowly and requires up to 12 mo to complete its life cycle, whereas in very warm prairie lakes it may take 3 mo or less.

Diaptomus forbesi has been lightly treated in the literature. In the study area, it was found in shallow, warm, and moderately saline (TDS = 131–1121 ppm) lakes. Although *D. forbesi* and *D. leptopus* were often found in nearby lakes, the *D. forbesi* lakes were usually more saline and contained more crustacean species at greater densities.

Eucyclops agilis was found only in relatively low-salinity lakes (TDS = 13–358 ppm) although it has been reported at salinities of from 12,000 to 20,000 ppm by Rawson and Moore (1944; as *Cyclops serrulatus*) and Whittaker and Fairbanks (1958).

Acanthocyclops vernalis, the most frequently occurring crustacean plankter in this study, occurred at salinities from 2 to 1121 ppm. It has been reported at much higher salinities (4270 ppm; Whittaker and Fairbanks 1944) and may occur in Seagrams Lake, Sask. (19,500) ppm. Reed (1962) found this to be the most frequently occurring cyclopoid in 165 far northern lakes and ponds. In the Great Lakes and some Okanagan lakes, *A. vernalis* was abundant only when *Diacyclops bicuspidatus thomasi* was not (Patalas 1972; Patalas and Salki 1973). In two lakes in this study, it has been shown that *A. vernalis* abundance declines in the presence of abundant *D. b. thomasi* (Anderson 1970a, 1972). In 45 ELA lakes and 32 central Ontario ponds, *A. vernalis* was more common in small, shallow lakes and *D. b. thomasi* in cold, deep, transparent lakes (Carter 1971; Patalas 1971). Although *D. b. thomasi* was found in colder, lower salinity lakes in the present study (TDS = 2–372 ppm; heat = 4.5–23.0 kcal/liter than was *A. vernalis* (TDS = 2–1121 ppm; heat = 3.8–30 kcal/liter), *D. b. thomasi* has been reported at salinities up to 4290 ppm (Whittaker and Fairbanks 1958) and may be the species reported at 10,000 ppm by Rawson and Moore (1944).

In only 8 of 124 lakes and ponds where *D. arcticus* occurred, was the total crustacean plankton density greater than 30 animals per liter. Five of the eight were warm, shallow lakes below 1400 m elevation where *D. arcticus* was a spring species and absent the rest of the year. In the other three, *D. arcticus* was sparsely represented. The general low abundance of other zooplankton species in *D. arcticus* communities, as well as in many *D. shoshone* communities, is undoubtedly due to the predatory feeding habits of these copepods (Anderson 1970c). Cyclopoids often have a similar effect on the communities, particularly in cold lakes and if fish are present (Table 7; Anderson 1972). *Gammarus lacustris* may have a similar effect on the plankton in certain cold, oligotrophic lakes where it occurs

TABLE 8. Crustacean plankton density, species composition and abundance

Lake no.	Name	Grid reference	date for Chem data	Elevation (*m*)	Area (*ha*)	Max known depth (*m*)	Secchi disc depth (*m*) max found	Field pH	TDS (*ppm*)
J 342	Skyline P.	11U/MJ379547	11.9.68	2094	4.0	1.5	+[d]	8.1	65
J 92	Cloudy L.	11U/MJ830151	7.9.67	2322	2.0	7.0	1.0	8.2	90
B 461	Norman L.	11U/NH068711	16.6.66	1968	1.5	5.0	+[d]	8.4	128
B 421	Totem L.	11U/NH257485	8.7.66	2165	1.2	4.0	1.4	8.4	78
B 291	Lo. Dolomite	11U/NH411270	29.8.67	2353	0.4	3.0	+[d]	8.6	89
B 174	Agnes L	11U/NG525960	3.8.66	2117	6.0	20.5	8.5	8.6	60
B 507	Larch val. E	11U/NG548867	2.8.66	2363	0.4	1.5	+[d]	8.4	80
B 68A	Larch val W.	11U/NG540866	2.8.66	2390	0.2	3.3	+[d]	8.3	65
Y 51	Wave P	11U/NH349146	9.9.69	2226	0.4	3.6	2.4	8.4	23•
Y 41A	Nr. Celeste	11U/NH336078	10.8.72	1976	0.2	2.0	+[d]	8.0	60
Y 28	Ptarmigan P	11U/NG207990	9.9.69	2014	0.8	2.0	+[d]	8.2	80
Y 23	up. Morning Glory	11U/NG440902	8.7.70	2006	1.7	4.0	+[d]	8.2	70
Y 22	mid-Morning Glory	11U/NG444903	8.7.70	1997	1.0	2.5	+[d]	8.2	76
Y 24	Linda L	11U/NG437909	8.7.70	2098	4.0	12.0	+[d]	8.2	93
Y 12	Victoria L	11U/NG474896	5.8.66	2225	0.4	4.5	+[d]	7.8	55
W 13	Carthew P	11U/TK817348	16.8.71	2159	0.8	0.5	+[d]	8.3	40
W 23	Crypt P	11U/TK919321	13.8.71	1713	2.7	2.0	+[d]	8.3	37
R 24	Millar P	11U/MG224587	29.6.70	1921	0.1	1.8	+[d]	–	–

[a]Footnotes as in Table 2.

(e.g. Storm Lake, Kootenay, Anderson and Raasveldt 1974).

Chydorus sphaericus is one of the most widely distributed crustacean species of North American zooplankton (e.g. Carl 1940; Patalas 1964), although it often occurs at low densities. It has been reported at salinities up to 20,000 ppm (Rawson and Moore 1944), and in the present study it was present throughout a salinity range of 2–6213 ppm, but not in Gooseberry Lake (29,800 ppm). *Bosmina longirostris* is another widespread species (e.g. Brandlova et al. 1972; Carter 1971; Mayhood et al. 1973) but this species is more truly planktonic than *C. sphaericus*. *Bosmina longirostris* often occurs at high densities, especially when fish are present (Brynildson and Kempinger 1973). It appears to be absent from highly saline waters in the study area (range = 30–513 ppm) and from warm, shallow waters (range = 4.0–26.0 kcal/liter). It was uncommon in alpine lakes, a point also noted by Patalas (1964). *Alona guttata* was also fairly common, though seldom abundant. Other *Alona* spp. were well represented, but rather uncommon. *Pleuroxus* spp. were also well represented, although occurring infrequently and at low densities, a pattern noted in other survey studies (e.g. Brandlova et al. 1972; Carl 1940).

As reported earlier (Anderson 1968; Hartland-Rowe and Anderson 1968), the occurrence of *Diaptomus victoriaensis* and *Artemiopsis stephanssoni* in the study area represent marked extensions to their previously known distributional ranges. The occurrence of *D. hirsutus* in Mt. Revelstoke National Park, B. C., and *Moina macrocopa* in Deadhorse Lake, Alta., also represent range extensions (Goulden 1968). The possible occurrence of *M. macrocopa* in central British Columbia was noted by Carl (1940). Two widely separated occurrences of *Ceriodaphnia acanthina* in the study area and earlier reports by Carl for B. C. indicate this species may be more widespread than originally thought (Brooks, in Edmondson 1959).

and some limnological features for 18 Group VII lakes and ponds.[a]

Heat content (*Kcal/liter*)	Crustacean plankton				*Alona guttata*	*Alona costata*	*Chydorus sphaericus*	*Daphnia rosea*	*Daphnia pulex*	*Daphnia schoedleri*	*Simocephalus vetulus*	*Scapholeberis kingi*	*Bosmina longirostris*	*Ceriodaphnia sp.*	Unident. cyclopoid nauplii	*Branchinecta paludosa*	*Gammarus lacustris*	Diptera larvae	misc. insect larvae	water mites	nematodes	rotifers
	Max No. per liter	Total No. spp.	Cladocera spp.	Copepoda spp.																		
5.5	0	0	0	0	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
9.6	0	0	0	0	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.
–	20.0[b]	5	4	1	.	.	3	.	.	.	1	3	.	2	1	.	.	.	.	.	.	.
4.1	0.3	1	1	0	.	.	1	.	.	.	.	.	.	.	.	.	.	2	1	1	.	1
9.7	0	0	0	0	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
8.3	0.1	1	1	0	.	.	.	.	1?	.	.	.	.	.	.	.	.	.	.	.	.	4
6.1	0.1	1	0	1	.	.	.	.	.	.	.	.	.	.	1	.	.	1	.	.	.	1
4.9	0	0	0	0	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	.	1
10.1	0	0	0	0	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.
8.0	0	1	0	0	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.
10.0[b]	0	0	0	0	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	.	1
8.0[b]	0.1	1	1	0	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	1	1	.
10.7	0.1	1	0	1	.	.	.	.	.	.	.	.	.	.	1	.	.	1	1	.	1	1
7.4	0.1	2	1	1	.	.	1	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.
5.5	0.1	1	0	1	.	.	.	.	.	.	.	.	.	.	1	.	.	.	1	.	.	.
14.5	12.5	8	7	0	2	2	3	1	1?[e]	1	.	.	1	.	.	2	.	.	.	.	.	3
11.4	0	0	0	0	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1
–	0	0	0	0	.	.	.	.	.	.	.	.	.	.	.	.	.	2	1	.	.	.

Recent work by Brandlova et al. (1972) and observations by J. Hrbáček (personal communication) indicate there are taxonomic problems concerning *Daphnia* spp. in the study area. There is little question that populations conforming closely to European specimens of *D. pulicaria* occur. Many puzzling populations, apparently near *D. rosea* and *D. g. mendotae*, were undoubtedly those commonly referred to as *D. longispina* in earlier studies. Further considerations are being given to taxonomic problems on the *pulex–middendorffiana–schoedleri–pulicaria* group and the *rosea–galeata–longispina* group. The single occurrences of *D. longiremis* and *D. parvula* seem to be small but not unexpected extensions of the distributional range as reported by Brooks (1957). The occurrence of *D. catawba* represents a second major westward extension in range since the publication of Brooks' monograph. It was also reported from southern Saskatchewan (Brooks, in Edmondson 1959).

Conclusions

The total of 97 crustacean species identified in the 340 lakes and ponds of this study is comparable to the totals found in other survey studies of similar numbers of waters in temperate North America. Of the 14 anostracan species known for Alberta (Hartland-Rowe 1965 and personal communication), 9 were found in this study. Twenty-one calanoid copepod species were found, of which 14 were common to the 25 known species for Saskatchewan (Wilson 1958; Anderson 1970d, 1971a). Of the 97 species identified here, 25 were single occurrences, and further studies will undoubtedly reveal infrequent occurrences of additional species. Many species which appear to be uncommon at the present time may turn out to be less uncommon when more lakes are sampled and studies are conducted throughout the year in other lakes.

It is likely that predator–prey relationships, competition, permanence of water body, heat, and extremes in salinity are the most important factors influencing the distribution of species. However, because all of the most commonly occurring species in this study are tolerant of or capable of adapting to a wide range of environmental conditions, the distributional patterns of certain species such as *Acanthocyclops vernalis* and *Diacyclops bicuspidatus thomasi* suggest that competition or predation may be of overriding importance. *Gammarus*, *Chaoborus*, *Hesperodiaptomus*, *D. b. thomasi*, and fish are all capable of exerting selective pressures on certain crustacean species through predation, especially in the simple aquatic environments characteristic of so many of the mountain lakes and ponds of this study (Anderson 1968, 1970a, 1970c, 1971b, 1972; Anderson and Raasveldt 1974).

In the waters surveyed here, the number of species per community increased with the complexity of aquatic habitat, where the number of ecological niches was larger. Complexity was usually higher at low altitudes, high temperatures, low water-renewal rates, and moderate salinity. However, the greatest zooplankton species diversity was characteristic of small waters, where frequent fluctuations in certain conditions together with habitat complexity fostered diversity by preventing certain species from becoming ecologically dominant in the community and by increasing the available number of ecological niches.

A number of similarities exist between high alpine lakes and ponds, and highly saline prairie lakes. Both are usually characterized by rather uniform aquatic habitats (e. g. few or no aquatic macrophytes) and a small number of ecological niches. The relatively small numbers of crustacean species present and the genera represented are often markedly similar, although the density of zooplankton in the saline lakes is usually higher and the total productivity is greater. In the study area, copepods from both types of waters are often characterized by large body size, dark coloration, relatively long generation times, and slow growth rates. These waters provide interesting possibilities for comparative physiological and ecological studies.

Acknowledgments

Material for this study was collected over a period of 9 yr, and often involved long and arduous hikes. I extend my thanks to those who assisted in the field, often under adverse weather conditions: A. Colbeck, D. Donald, J. Kilistoff, D. Krochak, G. Scott, B. Turner, C. Ward, Warden. Service and other National Parks personnel, several others whose help was acknowledged in earlier papers, and especially my son, S. Anderson, who has been my most frequent assistant and companion on the hundreds of field trips involved. I am grateful to D. Donald, G. Fabris, R. Hartland-Rowe, J. Kazmierski, L. Raasveldt, and G. White for providing certain specimens and data, and to Dr Hartland-Rowe for assistance with the Anostraca and Notostraca. Thanks are also due to R. Green for help in table preparation, and to Kathleen McFarlane for many hours of typing assistance. Laboratory space was provided by the Biology Department, University of Calgary.

Anderson, R. S. 1968. The zooplankton of five small mountain lakes in southwestern Alberta. Natl. Mus. Can. Nat. Hist. Pap. 39: 19 p.

1970a. Effects of rotenone on zooplankton communities and a study of their recovery patterns in two mountain lakes in Alberta. J. Fish. Res. Board Can. 27: 1335–1356.

1970b. The physical and chemical limnology of two mountain lakes in Banff National Park, Alberta. J. Fish. Res. Board Can. 27: 233–249.

1970c. Predator–prey relationships and predation rates for crustacean zooplankters from some lakes in western Canada. Can. J. Zool. 48: 1229–1240.

1970d. *Diaptomus* (*Leptodiaptomus*) *connexus* Light 1938 in Alberta and Saskatchewan. Can. J. Zool. 48: 41–47.

1971a. A *nomen novum* to replace the junior homonym, *Diaptomus* (*Leptodiaptomus*) *intermedius*, Anderson and Fabris 1970. Can. J. Zool. 49: 133.

1971b. Crustacean plankton of 146 alpine and subalpine lakes and ponds in western Canada. J. Fish. Res. Board Can. 28: 311–321.

1972. Zooplankton composition and change in an alpine lake. Int. Ver. Thor. Angew. Limnol. Verh. 18: 264–268.

Anderson, R. S., and L. G. Raasveldt. 1974. *Gammarus* predation and the possible effects of *Gammarus* and *Chaoborus* feeding on the zooplankton composition in some small lakes and ponds in western Canada. Can. Wildl. Serv. Occas. Pap. 18: 26 p.

Baird, D. M. 1963. A guide to geology for visitors in Canada's national parks. Nat. Hist. Parks Branch, Dep. Indian Aff. North Dev. Cat. No. R62-3163. 153 p.

Bajkov, A. 1929. Reports of the Jasper Park lakes investigations, 1925-26. VII. A study of the plankton. Contrib. Can. Biol. and Fish., Fish Res. Board Can., Ser. N. 4: 345–396.

Brandlova, J., Z. Brandl, and C. H. Fernando. 1972. The Cladocera of Ontario with remarks on some species and distribution. Can. J. Zool. 50: 1373–1403.

Brooks, J. L. 1957. The systematics of North American *Daphnia*. Mem. Conn. Acad. Arts Sci. 13: 1–180.

Brynildson, O. M., and J. J. Kempinger. 1973. Production, food, and harvest of trout in Nebish Lake, Wisconsin. Wis. Dep. Nat. Resour., Tech. Bull. 65: 1–20.

Carl, G. C. 1940. The distribution of Cladocera and free-living Copepoda in British Columbia. Ecol. Monogr. 10: 55–110.

Carter, J. C. H. 1971. Distribution and abundance of planktonic Crustacea in ponds near Georgian Bay (Ontario, Canada) in relation to hydrography and water chemistry. Arch. Hydrobiol. 68: 204–231.

Delorme, L. D. 1971. Freshwater ostracodes of Canada. Part V. Families Limnocytheridae, Loxoconchidae. Can. J. Zool. 49: 43–64.

Donald, D. B. 1971. The limnology and the plankton of three temporary ponds in Alberta. M.Sc. Thesis, Univ. Calg., Calgary Alta. 125 p.

Edmondson, W. T. [ed.] 1959. Fresh-water biology. 2nd ed. John Wiley and Sons, Inc., New York, N.Y. 1248 p.

Goulden, C. E. 1968. The systematics and evolution of the Moinidae. Trans. Am. Philos. Soc., N. Ser. 58: 1–101.

Hardy, W. G. [ed.] 1967. Alberta: a natural history. M. G. Hurtig Publishers, Edmonton, Alta. 343 p.

Hartland-Rowe, R. 1965. The Anostraca and Notostraca of Canada with some new distributional records. Can. Field Nat. 79: 185–189.

1967. *Eubranchipus intricatus* n.sp., a widely distributed North American fairy-shrimp, with a note on its ecology. Can. J. Zool. 45: 663–666.

Hartland-Rowe, R., and R. S. Anderson. 1968. An arctic fairy shrimp (*Artemiopsis stephanssoni* Johansen 1921) in southern Alberta, with a note on the genus *Artemiopsis*. Can. J. Zool. 46: 423–425.

Lötmarker, T. 1964. Studies on planktonic Crustacea in thirteen lakes in northern Sweden. Rep. Inst. Freshwater Res. Drottningholm 45: 113–189.

Mayhood, D. W., A. H. Kooyman, R. L. Hare, and R. D. Saunders. 1973. A limnological survey of some waters in southern Prince Albert National Park, Saskatchewan. Can. Wildl. Serv., Ms Rep. 171 p.

Patalas, K. 1964. The crustacean plankton communities in 52 lakes of different altitudinal zones of northern Colorado. Int. Ver. Theor. Angew. Limnol. Verh. 15: 719–726.

1969. Composition and horizontal distribution of crustacean plankton in Lake Ontario. J. Fish. Res. Board Can. 26: 2135–2164.

1971. Crustacean plankton communities in forty-five lakes in the Experimental Lakes Area, northwestern Ontario. J. Fish. Res. Board Can. 28: 231–244.

1972. Crustacean plankton and the eutrophication of St. Lawrence Great Lakes. J. Fish. Res. Board Can. 29: 1451–1462.

Patalas, K., and A. Salki. 1973. Crustacean plankton and the eutrophication of lakes in the Okanagan Valley, British Columbia. J. Fish. Res. Board Can. 30: 519–542.

Pennak, R. W. 1955. Comparative limnology of eight Colorado mountain lakes. Univ. Colo. Stud. Ser. Biol. 2: 75 p.

1957. Species composition of limnetic zooplankton communities. Limnol. Oceanogr. 2: 222–232.

Rawson, D. S. 1953. The limnology of Amethyst Lake, a high alpine type near Jasper, Alberta. Can. J. Zool. 31: 193–210.

Rawson, D. S., and J. E. Moore. 1944. The saline lakes of Saskatchewan. Can. J. Res. Ser. D 22: 141–201.

Reed, E. B. 1959. The distribution and ecology of fresh-water entomostraca in arctic and subarctic North America. Ph.D. Thesis. Univ. Sask. Saskatoon Sask. 152 p.

1962. Freshwater plankton Crustacea of the Colville River area, northern Alaska. Arctic. J. Arct. N. Am. 15: 27–50.

1964. Crustacean components of the limnetic communities of some Canadian lakes. Int. Ver. Theor. Angew. Limnol. Verh. 15: 691–699.

Reed, E. B., and J. R. Olive. 1956. Annual cycle of net plankton in a fluctuating north-central Colorado reservoir. Ecology 37: 713–719.

Rigler, F. H., and R. R. Langford. 1967. Congeneric occurrences of species of *Diaptomus* in southern Ontario lakes. Can. J. Zool. 45: 81–90.

Whittaker, R. H., and C. W. Fairbanks. 1958. A study of plankton copepod communities in the Columbia basin, southeastern Washington. Ecology 39: 46–65.

Wilson, M. S. 1958. New records and species of calanoid copepods from Saskatchewan and Louisiana. Can. J. Zool. 36: 489–497.

1972. Copepods of marine affinities from mountain lakes of western North America. Limnol. Oceanogr. 17: 762–763.

Factors Affecting Sockeye Salmon (*Oncorhynchus nerka*) Growth in Four Lakes of the Fraser River System[1]

J. C. GOODLAD, T. W. GJERNES

International Pacific Salmon Fisheries Commission
New Westminster, B.C.

AND E. L. BRANNON

College of Fisheries
University of Washington, Seattle, Wash. 98195, USA

GOODLAD, J. C., T. W. GJERNES, AND E. L. BRANNON. 1974. Factors affecting sockeye salmon (*Oncorhynchus nerka*) growth in four lakes of the Fraser River system. J. Fish. Res. Board Can. 31: 871–892.

Analysis of data from four sockeye rearing lakes of the Fraser River system for periods of up to 20 yr provided information on the relation of estimated fish density (female spawners/ha), temperature, and zooplankton standing crops to growth. The lakes differed widely in all attributes. Growth was inversely related to estimated population density in three of the lakes, but wide variations in growth at low density occurred in the fourth, a cold lake at high elevation with short growing season. In this lake, and to a lesser extent in another lake with short growing season, temperature during fry emergence and early lake residence accounted for much of the recorded fluctuation in growth. Reduced zooplankton abundance was associated with high sockeye density in two of the lakes with intermediate standing crops and greatest sockeye densities, but was not recorded in a lake of low standing crop and intermediate sockeye density. Sockeye feeding was found to be highly selective in one lake, and a limited proportion of the zooplankton standing crop was utilized. It is suggested that reduction in standing crop by grazing of juvenile sockeye, and associated decrease in growth, is greatest as the large zooplankters are progressively reduced in abundance. Further reduction in standing crop and in sockeye growth was suggested to proceed at a slower rate. Competition at high population density was concluded to be the factor most responsible for reducing sockeye growth.

GOODLAD, J. C., T. W. GJERNES, AND E. L. BRANNON. 1974. Factors affecting sockeye salmon (*Oncorhynchus nerka*) growth in four lakes of the Fraser River system. J. Fish. Res. Board Can. 31: 871–892.

L'analyse des données recueillies dans quatre lacs d'élevage de saumons nerka dans le régime du fleuve Fraser, sur des périodes allant jusqu'à 20 ans, ont fourni des renseignements sur la relation entre l'estimé de la densité des poissons (femelles reproductrices/ha), la température et la biomasse du zooplancton d'une part, et la croissance d'autre part. Les lacs varient considérablement dans tous leurs attributs. La croissance est en relation inverse de l'estimé de la densité de population dans trois des lacs, mais il se produit de fortes variations de croissance, avec faible densité de population, dans le quatrième, un lac froid de haute altitude et à courte saison de croissance. Dans ce lac et, à un degré moindre, dans un autre lac à courte saison de croissance, la température au moment de l'émergement des alevins et du bref séjour dans le lac est responsable de la plus grande partie des fluctuations de croissance. Une abondance réduite du zooplancton est associée à une forte densité de saumons nerka dans deux des lacs à biomasse intermédiaire et densité maximale de saumons nerka, mais ceci n'a pas été enrégistré dans un lac à faible biomasse et densité de saumons intermédiaire. On observe une alimentation très sélective chez les

---

[1] This paper, part of a special issue that comprises a comprehensive review of Limnology in Canada, was prepared to mark the 19th Congress of the International Association of Limnology (SIL), in Winnipeg, Man., during August 1974.

Printed in Canada (J3278)

saumons d'un lac et l'utilisation d'une petite proportion de la biomasse du zooplancton. Nous croyons que la diminution de la biomasse à la suite du broutage par les jeunes saumons nerka et la diminution de croissance qui s'ensuit sont à leur maximum à mesure qu'il y a diminution de l'abondance de gros organismes du zooplancton. On a des indications qu'une diminution ultérieure de la biomasse et de la croissance des saumons se poursuit à un rythme plus lent. On conclut que la concurrence, lorsque la densité de population est forte, est le facteur le plus important de diminution de croissance du saumon nerka.

Accepted January 11, 1974

THE sockeye salmon, *Oncorhynchus nerka* (Walbaum 1792), is an anadromous species of the family Salmonidae that occurs on both sides of the North Pacific from 43° N to 63° N latitude (Hart 1973). Sockeye are a valuable commercial fish and are exploited heavily. Adult sockeye migrate to the natal stream (or lake) in the summer and fall to spawn and die. Their offspring emerge from the gravel as fry and enter a lake where they remain for 1 or more years, later migrating to sea as smolts where they remain from 1½ to 3½ yr before returning as adults.

The sockeye salmon of the Fraser system are made up of many separate populations or races which are reproductively isolated (Royal 1953; Killick 1955). Virtually all Fraser River sockeye rear in a nursery lake for 1 yr and nearly 90% return from the sea in their fourth year (Killick and Clemens 1963). Fry of these races rear in specific nursery lakes and fluctuations in growth, both between and within lakes, have long been noted (Clutter and Whitesel 1956).

Many studies have been conducted on growth of sockeye in the lacustrine environment. Some have centered on the effect of fingerling abundance on growth (Burgner 1964), and others have examined growth and sockeye population density in relation to extent of lake utilization and zooplankton abundance (Johnson 1961, 1965; Ruggles 1965; Mathisen 1969) to assess effects of fish size on survival.

Similar studies are in progress at several of the 20 sockeye nursery lakes of the Fraser system. These have been of a long-term comparative nature rather than detailed examinations of single lakes. Although this approach lacks the precision of studies involving concurrent measures of fingerling density and size, feeding behavior, and zooplankton abundance, it has provided information on sockeye growth in a wide variety of conditions over a 20-yr period.

This paper examines sockeye growth as it relates to an index of sockeye population density (female spawners/ha), zooplankton, and temperature in four lakes — Cultus, Chilko, Fraser, and Shuswap — located between 49° N and 54° N latitude in southern British Columbia (Fig. 1).

Materials and Methods

Limnological studies of the four lakes have been carried out for periods ranging from 4 to 19 yr. Sampling stations, ranging from one to eight at each lake depending on lake size, have generally been visited monthly except during periods of winter ice-cover. Sampling procedure for measuring zooplankton standing crop has been consistent throughout, using a Wisconsin-type net of #10 bolting silk (aperture 158 μ) with a 25-cm diameter net opening. Replicate hauls (four or six) from a 30-m depth at each station have been preserved in formalin, washed for 1 min on a #10 silk screen to remove rotifers and phytoplankton, and centrifuged for 20 min to obtain a measure of settled volume. The average per haul was calculated, representing the volume of zooplankton in 1.5 m^3 of water, assuming 100% net efficiency. Sampling procedure and evaluation are described in more detail by Ward (1957). Beginning in 1970, both volume and dry weight (48 h @ 90 C) were recorded for each sample.

To assess possible food selectivity, the total dry weight of zooplankton was supplemented by separate measurements of four size-groups within the total sample. Zooplankton were washed through four sieves of different sizes (706, 409, 253, and 158 μ) and the quantity (dry weight) retained on each sieve recorded. Species retained on each sieve were identified. In some areas, littoral zone zooplankton were collected in a conical net of #10 bolting silk, 20 cm in diameter and 80 cm long, which filtered approximately 1 m^3 of water in a 30-m horizontal tow.

Each midlake zooplankton sample was accompanied by measurements of conductivity, water transparency, and lake temperature. Conductivity of a 2-1 surface water sample was measured with a Type RC conductivity bridge and readings were adjusted to a standard temperature of 25 C. Water transparency was determined by lowering a 25-cm diameter white Secchi disc in the shadow of the boat. Temperatures were measured by the use of bathythermographs (Bristol) or a thermistor (YSI 44TB). Records of temperature were made to a depth of 60 m or to the bottom if less than 60 m and recorded at 3-m intervals.

In addition, temperatures of certain major sockeye spawning streams were recorded with Bristol or Taylor 7-day clock recorders during the period of fry emergence. Temperature recorders were located approximately 1 km below Chilko Lake in Chilko River, nearly 11 km upstream from Fraser Lake (400 m below Francois Lake) in Stellako River, and nearly 3 km upstream from Shuswap Lake (7 km below Adams Lake) in Adams River.

Distribution of juvenile sockeye during lake residence was examined during 1971–73. Fish-targets were located with a 200 kHz Furuno Fg-200 echo sounder and sampled with a midwater trawl (3 × 6 m rectangular opening) operated at 0.8 m/s and fished to a depth of 45 m. A few echosounding studies were made during midday, but most were conducted after dark (1800–0200 h, depending on the season).

Midwater trawl catches at night of fish targets located by echo sounder were in all cases over 90% *O. nerka*. Daylight trawls were not attempted. In Cultus Lake, sticklebacks (*Gasterosteus aculeatus*) were collected in the same trawls with sockeye during winter, but rarely at other times of year. In Fraser Lake, only three chinook salmon (*O. tshawytscha*) and four whitefish (*Coregonus clupeaformis*) were collected with approximately 600 sockeye. In Shuswap Lake, only one squawfish (*Ptychocheilus oregonensis*) and two chinook salmon were collected with over 2000 ***O. nerka***. In some areas of this lake, three distinct size-groups within the *O. nerka* catch indicated the presence of both kokanee and sockey.

Samples of juvenile sockeye for examination of zooplankton species consumed were taken in 1970 before development of this midwater trawl. Fry were captured from onshore areas at midday with a small beach seine, and fingerlings from midlake areas at dusk were taken with a 175 × 10 m purse seine. Comparative zooplankton samples were taken at the same location and time (onshore) or 8 h earlier during daylight (midlake).

Sockeye spawning populations at Chilko, Fraser, and Shuswap lakes have been enumerated annually (Int. Pac. Salmon Fish. Comm. 1950–1973), based on tagging and dead recovery programs (Howard 1948; Schaefer 1951) in large streams, or live-counts in small streams. The proportion of female spawners and success of spawning (based on egg retention in dead females) was determined for each yearly run and the resulting number of "effective" female spawners calculated. The number of effective female spawners, considered here as an index of fingerlings produced, was divided by lake area to provide an index of finger-

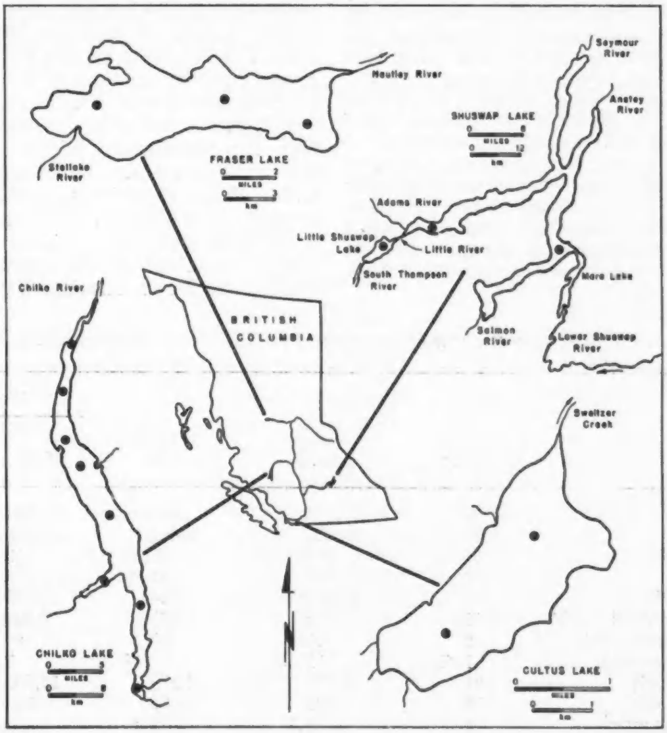

Nautley River
Stellako River
FRASER LAKE
MILES
km
Seymour River
Anstey River
SHUSWAP LAKE
MILES
km
Adams River
Little Shuswap Lake
Little River
South Thompson River
Mara Lake
Salmon River
Lower Shuswap River
Chilko River
BRITISH COLUMBIA
Sweltzer Creek
N
CHILKO LAKE
MILES
km
CULTUS LAKE
MILES
km

FIG. 1. Maps of Cultus, Chilko, Fraser, and Shuswap lakes and their location within the Fraser River system, British Columbia. Limnology stations noted (●).

ling abundance per hectare, hereafter termed density. A similar approach was used at Cultus Lake, although in this system the spawning run is enumerated at a weir before entering the lake. Lack of sizeable dead recovery from this lake spawning population precludes accurate estimates of egg retention. Foerster (1929) reported 5% of 57 females recovered from the 1925 spawning run were unspawned. In the present study, total counted females/ha were used as an index of subsequent fingerling density.

Kokanee spawning populations were enumerated for 11 yr (1953–1963) at Fraser and Shuswap, mainly by live-counts. At the other lakes, kokanee are not numerous (Cultus) or are extremely rare (Chilko).

Out-migrating sockeye smolt populations have been enumerated only at Cultus and Chilko. In both cases, migrating smolts were counted through a weir placed across the outlet stream. At Chilko, smolts were photographed at frequent intervals for abundance estimates, and individual fish passage across a known distance (a white board placed on the river bottom) was timed to give estimates of migration.

At Cultus, smolts passing through the weir entered a trap where they were measured by weight or water displacement, with frequent sample counts to determine the relation between weight (or volume) and numbers. In recent years, smolts leaving Cultus have been enumerated in a different way, by use of a continuously operating revolving sampler (Davis and Hiltz 1971) which diverts a constant small sample of the migrants (near 5%) to a trap for counting.

For this study, growth during freshwater residence has been determined primarily from scales of returning adult spawners, with some supplementary measurements of seaward migrating smolts. Seaward migrants have been preserved in formalin, and measured (fork length and weight) to determine total growth in fresh water.

Description of Lakes

PHYSICAL CHARACTERISTICS

The four sockeye rearing lakes studied differ widely in morphometry, elevation, and climatic conditions (Table 1). Cultus Lake, (Fig. 1) tributary to the lower Fraser River via Sweltzer Creek and the Vedder River, is situated in southwestern British Columbia approximately 113 km inland from the coast. It is a small lake (area 627 ha) at low elevation (41 m) with maximum depth of 42 m, situated in a glaciated U-valley between mountain ridges on either side. The physiography of the area has been described by Daly (1912) and the lake has been described in detail by Ricker (1937a). Cultus lies in a climatic region characterized by very high annual precipitation (127–381 cm), moderate annual range in temperatures, and mild winters (Chapman 1952). It rarely freezes over in winter.

Chilko Lake (Fig. 1) lies between the Pacific and Chilcotin ranges of the Coast Mountains, approximately 290 km northwest of Cultus Lake. Chilko is long (64 km) and narrow (maximum width 5.6 km), with an area of 20,030 ha and a maximum estimated depth of 366 m. The lake lies at a high elevation (1170 m) in a north-south valley with high mountains (up to 3050 m) on either side. The physiography of the surrounding area has been described by Davies (1948) and Holland (1964). Chilko is fed by large and small tributary streams, some lake-fed and others, particularly at its south end, fed by glacial meltwater. It is drained northward by the Chilko and Chilcotin rivers to the Fraser. The climate is one of moderate

TABLE 1. Physical characteristics of four sockeye rearing lakes in the Fraser River system.

	Cultus Lake	Chilko Lake	Fraser Lake	Shuswap Lake	
				Main Lake	Little Shuswap
Elevation (*m*)	41	1,170	640	348	348
Area (*ha*)	627	20,030	5,460	30,960	1,820
Maximum depth (*m*)	42	366[a]	30.5	162	64
Mean depth (*m*)	32	108	13.4	62	14
Volume ($m^3 \times 10^6$)	201	21,600	724	19,100	260
Mean annual runoff ($m^3 \times 10^6$)	112	1,373	1,072	8,700	8,700
Period of runoff record (*yr*)	5	10	19	54	54
Volume: runoff ratio (*yr*)	1.61	15.70	.68	2.20	.03
Watershed area (km^2)	83	1,975	6,270	15,600	15,700
Shoreline length (*km*)	14	176	65	320	21
Shore development ratio[b]	1.6	3.5	2.5	5.1	1.4

[a] Estimated.
[b] Length of shoreline ÷ circumference of circle with area equal to lake.

annual precipitation (64–76 cm), with cool summers and cold winters (4–5 mo below 0 C) (Chapman 1952). Chilko Lake almost always freezes over in winter.

Fraser Lake (Fig. 1) lies some 306 km north of Chilko Lake and 591 km northwest of Cultus Lake at an elevation of 640 m. The surrounding Nechako Plateau area has been described by Armstrong (1949). With an area of 5460 ha (Table 1), Fraser is nearly 9 times the area of Cultus Lake but is the shallowest of the lakes studied (maximum depth of only 30.5 m). It receives inflow mainly from Stellako and Endako rivers entering its western end and drains to the east via the Nautley and Nechako rivers to the Fraser River. The climate of the area is one of low annual precipitation (38–51 cm), short summers, and cold winters (4–5 mo below 0 C). Like Chilko, Fraser Lake usually freezes over in winter.

Shuswap Lake (Fig. 1), which lies east of the Fraser River, is part of the Thompson River watershed in the south-central portion of British Columbia. Drainage from this large, multibasin main lake flows through a small outlet basin, Little Shuswap Lake, then southwest via the South Thompson and Thompson rivers to join the Fraser River. It is the largest in area of the lakes studied (nearly 31,000 ha), with a maximum depth of 162 m (Table 1). To this, Little Shuswap, with a maximum depth of 64 m, adds an area of 1800 ha. Streams entering Shuswap range from small creeks to large rivers, some of which are lake-fed. With a high annual runoff, the theoretical flushing rate of the large basin of Shuswap is 2.2 yr: in contrast, that of Little Shuswap is only 0.03 yr (11 days). Shuswap lies at an elevation of 348 m within the southern Interior Plateau in an area described by Holland (1964) and Daly (1915). The climate is characterized by warm summers, moderately short winters (3–5 mo below 0 C), and moderate to low annual precipitation (51–76 cm) (Chapman 1952). Winter ice-cover occurs frequently but may not include the whole lake.

WATER TRANSPARENCY AND CONDUCTIVITY

Secchi disc measurements of water transparency varied both between and within lakes (Table 2). The four lakes, ranked in decreasing order of average seasonal transparency, were Cultus (10.5

TABLE 2. Water transparency and conductivity of four sockeye rearing lakes in the Fraser River system.

	Cultus Lake	Chilko Lake		Fraser Lake		Shuswap Lake	
	Midlake stns.	Uplake	Outlet	Uplake	Outlet	Uplake	Outlet
				Transparency (m)			
Range[a]	3–17	1–17	4–18	2–6	3–7	2–16	2–14
Monthly mean maximum	12.1 (Aug.–Sept.)	11.6 (May)	11.4 (May)	5.6 (Nov.)	6.4 (May)	12.4 (Apr.)	10.8 (Apr.)
Monthly mean minimum	5.0 (Jan.)	3.8 (Sept.)	6.9 (Sept.)	2.7 (May)	4.6 (Oct.)	5.5 (June)	7.1 (June)
May–October mean	10.5	6.8	8.5	4.4	5.7	7.3	8.2
No. years	6	11		3		14	
				Conductivity (μmho/cm^2 @ 25 C)			
Range[a]	140–180	46–58	53–62	84–106	87–100	85–114	55–106
Monthly mean maximum	180.0 (March)	55.6 (May)	56.4 (June)	–	–	103.6 (June)	89.6 (May)
Monthly mean minimum	156.5 (May)	53.0 (June–July)	54.5 (Apr.–Oct.)	–	–	91.3 (Oct.)	72.3 (Sept.)
May–October mean	167.2	53.9	55.4	94.0	95.6	95.0	79.8
No. years	3	7		3		8	
				Morphoedaphic index[b]			
	5.2	0.5		7.7		1.4	

[a] Range of individual measurements.

[b] Conductivity at 25 C divided by mean depth in meters.

m), Chilko (8.5 m), Shuswap (8.2 m) and Fraser (5.7 m). Seasonal patterns of transparency also differed between lakes, reflecting climatic and physiographic differences. Cultus Lake is clearest in late fall, and least transparent in winter due to high rainfall, whereas Chilko is least transparent in late summer because of glacial meltwater; Shuswap and Fraser are least transparent in early summer during the period of peak runoff. At Chilko and Shuswap, the outlet station averaged higher transparency with less fluctuation than uplake stations.

Conductivity of surface water samples from the four study lakes ranged from a high of 167 μmho/cm² at Cultus to a low of 55 μmho/cm² at Chilko (Table 2). The seasonal patterns of change in conductivity, like those of transparency, also differ between lakes. Cultus conductivity is highest in March and lowest in May, whereas Shuswap reaches a maximum in May–June and a minimum in September–October; little seasonal variation in conductivity occurs at Chilko, and measurements are inadequate to assess that of Fraser. The greatest absolute variation in conductivity has been recorded in the outlet region of Shuswap (55–106 μmho/cm²).

The morphoedaphic index, which in this study has been calculated as conductivity (instead of total dissolved solids as defined by Ryder 1965) divided by mean depth, indicates Fraser Lake would be most productive, followed by Cultus, Shuswap, and Chilko in decreasing order of productivity (Table 2).

Lake Water Temperatures

Plots of seasonal isotherms for the four lakes (Fig. 2) indicate similar thermal structure of the two southern lakes, Cultus and Shuswap, and certain similarities between the two more northerly lakes, Chilko and Fraser. The thermal regime of Cultus was described in detail by Ricker (1937a). During winter, Cultus is usually isothermal at 4–5 C, whereas there is a marked thermal inversion at Shuswap with the upper 15–20 m remaining at less than 4 C until late March. A narrow thermocline

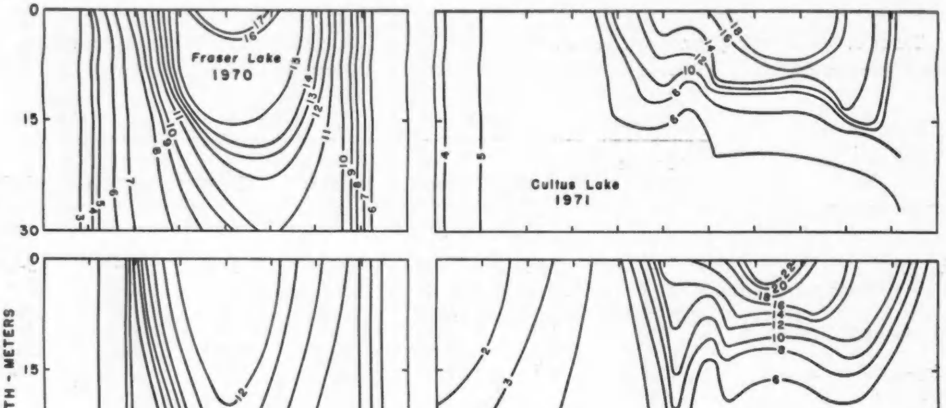


Fig. 2. Seasonal temperature isotherms of Cultus, Chilko, Fraser, and Shuswap lakes.

occurs at a depth of approximately 5 m at Cultus by May and about a month later at Shuswap. During summer the isotherms of Cultus are remarkably similar to those of the upper 30 m of Shuswap Lake. At both lakes the thermocline gradually widens and by late summer extends from 5 to 10 m. By late October thermal stratification is breaking down and both lakes are isothermal in late November, with Cultus at 6 C and Shuswap at 4 C.

In contrast to Shuswap and Cultus, Fraser and Chilko are subject to strong wind action in the spring. As a result, by mid-July the epilimnion extends to a depth of 15 m at Fraser and to almost 30 m in Chilko. In summer, epilimnion temperatures are higher at Fraser than at Chilko because of its lower elevation, and because of the large inflow (via Stellako River) of water warmed in Francois Lake, 11 km upstream. At both lakes, thermal stratification starts to break down by early October. By mid-October Fraser is isothermal at 10 C whereas at Chilko the epilimnion at 8 C extends to 45 m. Fraser and the upper 60 m of Chilko are isothermal at 5–6 C by early November.

To assess year-to-year temperature fluctuations, temperatures were examined for each lake for a fixed period, May 15 to October 15, each year (Table 3). The outlet basin of Shuswap Lake, Little Shuswap, has been included for comparison. Surface temperatures (0–9 m) of these lakes are closely related to elevation and growing season, with Cultus the warmest at 15.5 C (elevation 41 m) and Chilko the coolest at 9.0 C (elevation 1170 m). Deeper temperatures do not follow the same pattern, however. Warming of deeper waters appears to be a function of rapid flushing rate at Little Shuswap, wind action at Chilko, and both at Fraser. The greatest year-to-year variation in water temperature has occurred in Chilko, where both 0–9 m and 12–27 m mean temperatures have varied by approximately 4 C.

The May 15–October 15 temperatures provided comparison between and within lakes for a fixed 21-wk period, but did not necessarily indicate the duration of probable growth in all lakes. Growing season, estimated as the time between fry emergence and lake cooling to 5 C, appears to be considerably longer than this at two of the study lakes:

Lake	Average peak of fry emergence	Time to fall cooling (5 C)
Cultus	April 27	36 wk
Shuswap	May 13	30 wk
Fraser	May 17	25 wk
Chilko	May 25	23 wk

CRUSTACEAN ZOOPLANKTON

Zooplankters commonly found in the open waters differ between the four lakes (Table 4). Cultus and Chilko support a restricted number of species (only six per lake) and in each lake, one of the copepods is the single most abundant species — *Cyclops bicuspidatus thomasi* in Cultus, *Diaptomus ashlandi* in Chilko. In contrast, Fraser and Shuswap each support 11 common species, and in each lake *Daphnia* is among the most abundant — *D. galeata* in Fraser, *D. thorata* in Shuswap.

Examination of the average size of each species (based on data given by Edmondson 1959) in each lake reveals that Fraser supports larger species than the other lakes. Fraser contains the largest *Daphnia* (*D. galeata*), the largest *Cyclops* (*C.*

TABLE 3. Range and mean of May 15–October 15 water temperatures at four sockeye rearing lakes in the Fraser system.

Lake		Temperature (*C*) 0–9 m	12–27 m	0–27 m
Cultus — midlake	Range	13.9–16.9	6.2–8.8	9.4–11.7
(12 yr)	Mean	15.5	7.5	10.7
Shuswap — outlet	Range	11.8–16.2	5.6–7.5	8.3–10.8
(18 yr)	Mean	14.2	6.6	9.6
Little Shuswap — midlake	Range	12.3–14.9	11.4–13.7	11.8–14.2
(5 yr)	Mean	13.3	12.4	12.8
Fraser — midlake	Range	11.6–13.1[a]	8.9–11.0[a]	10.0–11.8[a]
(5 partial yr)	Mean	12.2	9.9	10.9
Chilko — outlet	Range	7.2–11.6	6.0–9.8	6.5–10.1
(14 yr)	Mean	9.0	7.8	8.3

[a] Estimated.

scutifer) and *Diaptomus* (*D. pribilofensis*), and is the only lake to support the large *Heterocope septentrionalis* (Table 4).

The seasonal pattern of zooplankton dry weights for a single year at each lake are presented in Fig. 3. Samples are from midlake stations in Cultus and Fraser, and from near-outlet stations at Chilko and Shuswap. At all lakes, the smallest sieve (158 μ) retained all nauplii and small copepodids, the next largest sieve (253 μ) usually retained the bulk of the *Cyclops*, *Diaptomus*, *Bosmina*, and a few *Daphnia*. The 409 μ screen retained the larger *Diaptomus*, *Bosmina*, and a few *Cyclops*, as well as *Daphnia* and small *Epischura*. The largest sieve, 706 μ, retained large *Daphnia*, *Epischura*, *Leptodora* and, in Fraser Lake, *Heterocope*.

Zooplankton was most abundant in June 1971 in Fraser (110 mg), dropping thereafter to a low of 15 mg in November (Fig. 3). Small plankters made up the majority of the June bloom, whereas later in the season larger plankters retained on the two largest sieves predominated. At Chilko and Shuswap, small blooms of zooplankton (20 mg or less) occurred in both June and September. In both lakes, organisms retained on the two smallest sieves predominated throughout the season. In contrast, large zooplankters on the 706 and 409 μ sieves predominated through most of the season at Cultus. Blooms of up to 50 mg occurred in late March and late May, decreased in June and July, and increased again in October.

The annual standing crop of zooplankton, measured as settled volume per 30-m haul averaged from June 15 to October 15, has been measured for several years and provides information as to the variation and average level for each lake (Table 5). Fraser has averaged the largest standing crop of zooplankton (1.73 cm^3) and Chilko the lowest (0.46 cm^3), for a nearly fourfold difference between lakes. Year-to-year variation in standing crops has been greatest in the two lakes of intermediate zooplankton levels — a fourfold variation at Cultus (0.68–2.77 cm^3) and a 3.8-fold variation at Shuswap (0.46–1.76 cm^3).

TABLE 4. Relative abundance (rare +, common ++, abundant +++) of crustacean zooplankters taken in #10 silk net samples from the open waters of four sockeye rearing lakes, Fraser River system (species arranged in order of increasing size).

Species	♀ Range in length (*mm*)[a]	Cultus Lake	Chilko Lake	Shuswap Lake	Fraser Lake
Cladocera					
Bosmina coregoni longispina (Leydig)[b]	±0.4[c]	+	++	+	++
Bosmina longirostris (O. F. Müller)	0.3–0.5[c]	–	–	+	–
Diaphanosoma leuchtenbergianum Fischer	0.9–1.2	–	–	+	+
Daphnia longiremis Sars	0.8–1.2	+	+	+	+
Daphnia rosea Sars emend. Richard[d]	1.2–1.6	++	–	–	–
Daphnia sp.[e]	to 1.85[f]	–	+	–	–
Daphnia thorata Forbes	1.3–1.8	–	–	+++	–
Daphnia galeata Sars *mendotae* Birge	1.3–3.0	–	–	–	+++
Holopedium gibberum Zaddach	1.5–2.2	–	–	+	–
Sida crystallina (O. F. Müller)	3.0–4.0	–	–	+	+
Leptodora kindtii (Focke)	7–18.0	+	–	+	+
Copepoda					
Cyclops bicuspidatus thomasi S. A. Forbes	0.9–1.2	+++	++	+++	–
Cyclops scutifer Sars	1.3–1.9	–	–	–	+++
Diaptomus ashlandi Marsh	0.9–1.4	–	+++	+++	+++
Diaptomus pribilofensis Juday and Muttkowski	1.1–1.8	–	–	–	++
Epischura nevadensis Lilljeborg	1.3–2.5	+	+	+	+
Heterocope septentrionalis Juday and Muttkowski	3.0–4.0	–	–	–	+

[a] As reported by Edmondson (1959) except where noted.

[b] Classification of Deevey and Deevey (1971). All others from classification of Edmondson (1959).

[c] Ward and Whipple (1918).

[d] Reported previously as *Daphnia pulex* (Foerster 1925) but considered to have been incorrect (W. E. Ricker personal communication).

[e] Species not yet identified (K. Patalas personal communication).

[f] From present study.

Comparison of the two measures of zooplankton standing crop, settled volume and dry weight, indicate differences between lakes are underestimated by measurements of volume. A settled volume of 1.00 cm^3 weighs an average of 25.0 mg at Cultus, 27.0 mg at Shuswap, 32.5 mg at Chilko, and 43.5 mg at Fraser. Conversion of average settled volumes to dry weights therefore indicates a fivefold difference between Fraser (75 mg) and Chilko (15 mg). Year-to-year variations in standing crops within lakes may also have been underestimated by volume measurements. The weight-to-volume ratio has remained relatively constant for each lake, but year-to-year variations in standing crop within each lake have been relatively small during the 3 yr analyzed.

The level of zooplankton standing crop at each lake appears related to the morphoedaphic index, with the shallow basin of Fraser having the highest average standing crop and highest index 7.7 (Table 2). At the other extreme, Chilko most resembles the classical "oligotrophic type" lake with low standing crop and a low morphoedaphic index of 0.5. In these four lakes, mean zooplankton standing crops also appear associated with average lake temperature (0–27 m), with higher standing crops in the warmer temperatures (>9.5 C) of Fraser, Cultus, and Shuswap than in the cool temperatures (8.3 C) of Chilko (Table 3). Differences in zooplankton standing crops between lakes do not appear related to the general level of water transparency. Cultus and Fraser, with the highest (10.8 m) and

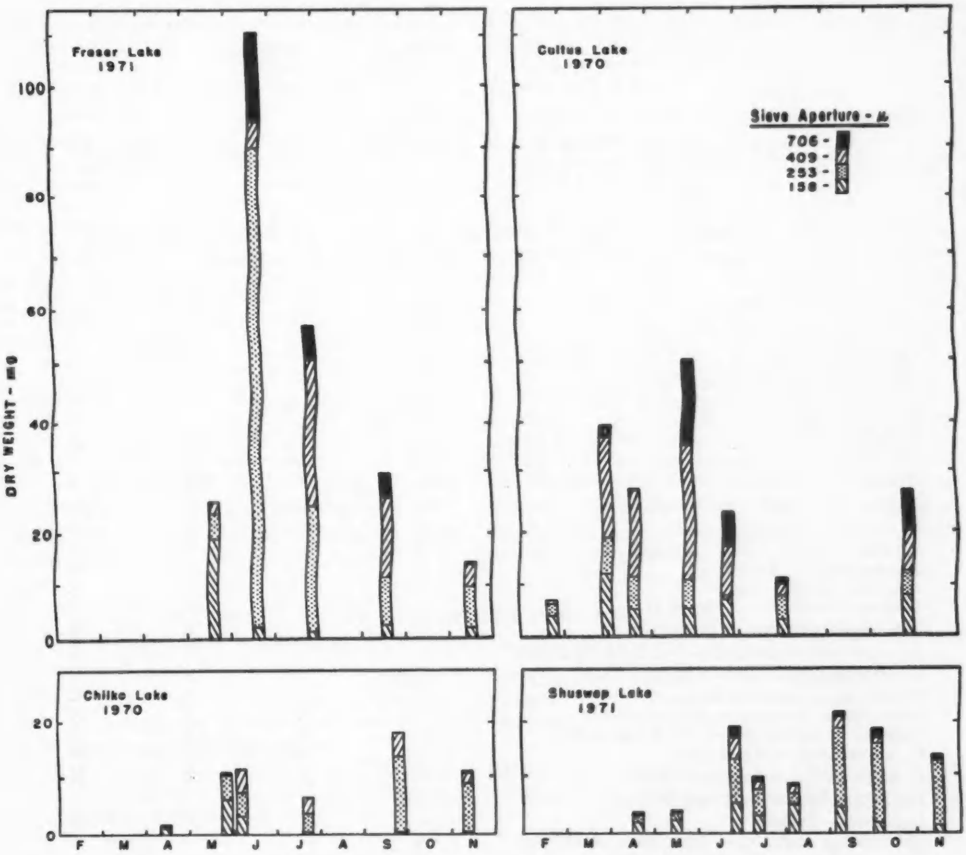


FIG. 3. Seasonal zooplankton standing crops at Cultus, Chilko, Fraser, and Shuswap lakes.

lowest (5.0 m) average transparency, respectively, have higher zooplankton standing crops than Chilko or Shuswap.

FISH SPECIES

Of the four lakes, Chilko has the smallest number of common fish species (8), and Fraser the largest (18) (Table 6). Little is known con cerning relative abundance of species other than sockeye and their landlocked counterpart, kokanee (*O. nerka*).

In 7 yr of gillnetting studies at Cultus Lake, Foerster and Ricker (1941) report capturing over 10,000 northern squawfish (*Ptychocheilus oregonensis*), more than 2000 each of cutthroat trout (*Salmo clarki clarki*), residual sockeye (or kokanee), and largescale suckers (*Catostomus macrocheilus*), several hundred Dolly Varden (*Salvelinus malma*), coho salmon (*O. kisutch*), and prickly sculpin (*Cottus asper*), and less than 100 each of mountain whitefish (*Prosopium williamsoni*) and peamouth (*Mylocheilus caurinus*).

In Chilko Lake, limited gillnetting for large fish during 1960 and 1961 captured predominantly Dolly Varden (*S. malma*), rainbow trout (*Salmo gairdneri*), and mountain whitefish (*P. williamsoni*). Kokanee are rarely present in Chilko.

In Shuswap Lake, rainbow trout are more abundant in sport catches than other predator species (Ward and Larkin 1964). Kokanee pop-

TABLE 5. Range and mean yearly (June 15–Oct. 15) standing crop of zooplankton in the four study lakes.

	Cultus Lake	Chilko Lake	Shuswap Lake	Fraser Lake
No. years	4	15	19	4
Range in yearly volume (*cm*^{3})	0.68–2.77	0.30–0.83	0.46–1.76	1.46–1.84
Mean all years (*cm*^{3})	1.54	0.46	1.12	1.73

TABLE 6. Fish species recorded in four sockeye rearing lakes of the Fraser River system.

Species	Cultus Lake	Chilko Lake	Fraser Lake	Shuswap Lake
Coregonus clupeaformis — Lake whitefish	–	–	X	X
Oncorhynchus gorbuscha — Pink salmon	X	–	–	–
O. nerka — Kokanee (landlocked)	Rare	Very Rare	X	X
O. keta — Chum salmon	X	–	–	–
O. kisutch — Coho salmon	X	–	–	X
O. tshawytscha — Chinook salmon	X	Rare	X	X
Prosopium williamsoni — Mountain whitefish	X	X	X	X
Salmo clarki clarki — Cutthroat trout	X	–	–	–
S. gairdneri — Rainbow trout	X	X	X	X
Salvelinus malma — Dolly Varden	X	X	X	X
S. namaycush — Lake trout	–	–	X	X
Cyprinus carpio — Carp	–	–	–	X
Couesius plumbeus — Lake chub	–	–	X	–
Mylocheilus caurinus — Peamouth	X	–	X	X
Ptychocheilus oregonensis — Northern squawfish	X	–	X	X
Rhinichthys cataractae — Longnose dace	X	X	X	–
R. falcatus — Leopard dace	X	–	X	X
Richardonius balteatus — Redside shiner	X	X	X	X
Catostomus catostomus — Longnose sucker	–	X	X	X
C. commersoni — White sucker	–	–	X	–
C. macrocheilus — Largescale sucker	X	X	X	X
Ictalurus nebulosus — Brown bullhead	Rare	–	–	–
Lota lota — Burbot	–	–	X	X
Gasterosteus aculeatus — Threespine stickleback	X	–	–	–
Cottus aleuticus — Coastrange sculpin	X	–	–	–
C. asper — Prickly sculpin	X	X	X	X

ulations are present in both Shuswap and Fraser and average 26,000 spawners in Fraser Lake tributaries (rarely over 100,000), and usually from 100,000 to 300,000 in Shuswap Lake tributaries.

Sockeye spawning populations have been enumerated annually at each lake.

Sockeye

SPAWNING POPULATIONS AND CALCULATED INDEX OF DENSITY

In most races of Fraser sockeye, a large (or "dominant") run returns every fourth year, with runs in the 3 intervening years usually much smaller in number (Ricker 1950; Ward and Larkin 1964). As most Fraser sockeye mature at age 4, each of the four "cycles" is relatively independent of the other. This cyclic pattern of abundance causes wide variations in spawning populations between years at one lake, as well as between lakes (Table 7). Females have formed an average of 53–57% of the adult escapements to Chilko, Fraser, and Shuswap. and a slightly higher estimated percentage at Cultus.

At Cultus Lake, annual runs of female spawners have ranged from 1600 to a high of 32,000 and have averaged nearly 11,000 during the last 24 yr of enumeration. Population density, based on female spawners, averaged higher at Cultus than the other lakes studied — 17.4 females/ha.

At Chilko Lake, the entire run (except lake spawners) spawns in the outlet river at the north end of the lake. Spawning runs (effective females) have ranged from 10,000 to 328,000 and averaged 109,000 during the past 24 yr. Population density has ranged from less than 1 to more than 16 females/ha, averaging 5.5 females/ha.

Most of the Fraser Lake sockeye run spawns in Stellako River at the west end of the lake. Numbers of effective female spawners have ranged from 14,000 to 78,000 and averaged 34,000 during the past 24 yr. Population density has varied least in Fraser, ranging from 2.5 to 14.2 females/ha and averaging 6.2 females/ha.

The most marked cyclic fluctuation in abundance occurs in the sockeye runs to Shuswap Lake. Here, the majority spawn in Adams and Little rivers (Fig. 1) but runs of up to 40,000 females also utilize Seymour River, and smaller numbers spawn in other tributaries. The total number of effective female spawners per year has ranged from 1,166,000 in the large cycle years down to less than 2000 in intervening years, with an average of 248,000 during the period from 1949 to 1972. This has led to marked variation in density, from 0.05 to 35.6 females/ha.

SMOLT POPULATIONS AND CALCULATED DENSITY

Smolt populations have been enumerated only at Cultus and Chilko lakes, with as many as 4 million from the former and 35 million from the latter. However, because of its much smaller area, the maximum density of smolts has been much higher in Cultus (6300/ha) than in Chilko (1700/ha), based on total lake areas.

To assess the use of female spawners as an index of subsequent juvenile abundance, smolt population size was tested against number of females. Comparison for 20 yr at Chilko and 16 yr at Cultus provided correlation coefficients of $r = 0.89$ ($P < .01$) and 0.42 ($P < .10$), respectively, indicating a much greater accuracy in predicting juvenile abundance from spawners at Chilko than at Cultus. Production of smolts per female has been slightly lower and much more variable at Cultus than at Chilko. Based on 16 yr at Cultus, the number of smolts per female has averaged 109 and ranged from 34 to 229 (nearly sevenfold), whereas for 20 yr at Chilko, smolts produced per female have averaged 141 and varied less than threefold (from 85 to 210). The situation in Fraser and Shuswap is not known, but the possibility of unknown variability in juvenile abundance as a function of female abundance both within and between lakes should be kept in mind.

TABLE 7. Sockeye female spawning populations, 1949–1972.

	Cultus Lake	Chilko Lake	Fraser Lake	Shuswap Lake
Effective females (*thousands*)				
Range	1.6–32.0	10.4–327.9	13.7–77.7	1.7–1165.8
Mean	10.9	109.2	34.0	248.3
Density (♀/*ha*)				
Range	2.6–51.0	0.5–16.4	2.5–14.2	0.05–35.6
Mean	17.4	5.5	6.2	7.6

DISTRIBUTION IN LAKES

On first entering Fraser and Shuswap lakes, fry remain near the entrance point for some time. Once movement is initiated the fry migrate at a rate of approximately 1 km/day. Migration was observed near shore (Chilko and Shuswap), through the limnetic area without littoral residence (Cultus), or by a combination of both (Fraser).

The horizontal distribution of sockeye fry and fingerlings in the limnetic zone, as determined by echo sounding, was relatively uniform only at Cultus. Distribution of sockeye fingerlings in the limnetic zone has not been assessed by echo sounding at Chilko. However, tow-netting (after the method of Johnson 1956) in August 1957 indicated higher density near the point of fry entry at the north end of the lake with progressively decreasing densities towards the south. In October 1957, very high catches were made at the north end, small catches in the midlake areas, and moderately higher catches in both arms of the southern portion of the lake.

In Fraser, once the fry moved offshore they concentrated in the vicinity of three deeper areas located from west to east along the lake. Later in the year (October–November), densities were low in the western area of the lake but high in the central and eastern areas. Echo sounding at Shuswap in 1971, 1972, and 1973 showed that in a year of high sockeye abundance (1971) there were high densities in the Adams and Salmon river arms, particularly near Adams River (where the fry originated). In a year of intermediate sockeye abundance (1972) the same arms had moderately high densities. In 1973 when the sockeye population was very low there were rather uniform low densities throughout the entire system. Acoustic surveys in 1972 and 1973 in Little Shuswap showed that sockeye were distributed throughout the area of the lake deeper than 15 m, but were not found in the extensive shallows (< 15 m) near the inlet and outlet. Heaviest concentrations of sockeye were found in the areas of greatest depth (> 40 m).

Except for Cultus, where fry emerge from beach spawning areas directly into the lake and apparently descend to deeper water, newly emerged fry utilized surface layers during daylight, and surface or near-surface layers at night (Table 8).

Vertical distribution of advanced fry and fingerlings in the limnetic zone was not monitored extensively during daylight. Limited echo sounding during the day at Fraser showed targets at a depth of approximately 15–25 m from July to November. As trawling was not attempted during daylight, targets were not identified but are presumed to be sockeye. Daylight echo sounding at Shuswap in October showed targets within the bottom 10 m of a shallow (40 m) region near the outlet but in deep basins (> 100 m) targets were found at a depth of 55 m. The vertical distribution of sockeye in the limnetic zone of Chilko has not been examined, but some sockeye activity has been observed at the surface during the day from July to October. Although daylight echo sounding has not been extensive, the two-layer distribution of sockeye observed at Babine Lake (Narver 1970) and Lake Washington (Woodey 1972) has not been observed in the four Fraser River system lakes studied.

Night distribution of fingerlings has been studied more extensively and indicates a progressively deeper and wider vertical distribution in the lakes

TABLE 8. Depth (*m*) of greatest concentration of juvenile sockeye at night from echo sounding.

Month	Cultus Lake	Fraser Lake	Little Shuswap Lake	Shuswap Lake	
				Outlet	Uplake
May	9–17		0–15		
June		0–9	0–12		6–9 to 9–15
July		9–15	3–24		
Aug.	12–40		9–18		6–18 to 9–18
Sept.	15–40	9–27	9–18	6–15	9–17 to 14–20
Oct.			3–30	18–33	18–33 to 20–33
Nov.	9–40	5–30		12–27	21–55 to 30–76
Dec.					
Jan.	15–30				
Feb.					
Mar.					0–12
Apr.	6–40				
Bottom depth	40	30	30	40	>100

until late summer or fall (Table 8). In the spring, prior to leaving the lake, pre-smolts in Cultus were found within 6 m of the bottom during daylight, but ranged from surface to bottom at night. In contrast, pre-smolts in Shuswap remained within the top 12 m of the lake at night. In all lakes studied, sockeye fry and fingerlings were rarely found in temperatures exceeding 15 C.

Vertical distribution of sockeye was monitored at dusk or dawn, but observations and surface or near-surface catches at dusk in trawls (Chilko) and purse seines (Fraser) indicate that sockeye migrate toward the surface for feeding as described at Babine (Narver 1970).

FEEDING

Numerous studies have documented the importance of crustacean zooplankton as food in all sockeye rearing lakes, and in several lakes selective use of this food supply by sockeye has been recorded (Narver 1970; Woodey 1972). The food of juvenile sockeye in Cultus Lake has previously been described by Foerster (1925) and evidence of selective feeding behavior noted (Ricker 1937b).

The present studies, conducted at Fraser Lake, assessed feeding in a lake of high standing crop (1.73 cm^3) in years of moderate sockeye density (4.9 female spawners/ha). In the 2 yr of study, sockeye emergence at Fraser coincided with the spring zooplankton bloom and zooplankton was an abundant food item in fry stomachs. However, from April to early June, fry captured from onshore areas as they were migrating throughout the lake also contained small chironomid pupae, which formed 40–90% of the bulk of stomach contents (Fig. 4). Measurement of zooplankters consumed by the young fry in April and May showed an apparent selection of medium size organisms; a positive but low electivity index (Ivlev 1961) was calculated for zooplankters of the size that would be retained on the 253 μ sieve (Table 9). By June 5 a definite selection of the largest organisms available (409 μ sieve) was evident.

In late summer, sockeye fingerlings strongly selected the largest zooplankters present in the population (Table 9 and Fig. 4). In August 1970 the number of large zooplankters was quite low; only 2% of the zooplankters were retained on the largest (706 μ) sieve. At this time some smaller zooplankters were eaten by sockeye fingerlings, but 60% by number of their diet was still from 2% of the standing crop. By late fall, 90% of the diet of sockeye fingerlings was derived from zooplankters that made up only 4% of the standing crop. In terms of total bulk, the proportion of the diet contributed by larger zooplankters was even greater.

From late August until late fall, *Daphnia* was the most abundant zooplankter retained on the 706 μ sieve and was also by far the most abundant organism found in sockeye stomachs. There were also many smaller *Daphnia* (409 μ sieve) in the plankton during this period, but the larger individuals were selected. In July 1971, *Heterocope* was the most abundant species retained on the 706 μ sieve and was virtually the only organism found in sockeye stomachs. Thus, after a short limnetic residence in Fraser Lake, sockeye fingerlings strongly selected the large (706 μ sieve) zooplankters.

GROWTH

Because smolts have not been sampled consistently at all study lakes, the number of freshwater circuli on scales of returning adults has been used as an index of lake growth. As described by Clutter and Whitesel (1956), the number of scale circuli formed in fresh water is related to both length and weight of seaward-migrating smolts. Some difference in circulus count at a given fish size is evident between smolts of certain different races of sockeye. For the four races in the present study, the only consistent difference was between Chilko and the other three races, the former race averaging 1.0 circulus less than the others at a given fish size.

In many cases, a small number of scale circuli is formed before migration but after the winter annulus, resulting in two areas of freshwater growth on the scales — growth to the annulus and "spring growth." In this study, spring growth has not been included in the total circulus counts, because spring growth is frequently greater on scales with few pre-annulus circuli (Foerster 1968) and tends to mask low growth rates in certain years.

Freshwater growth of sockeye has been greatest in Fraser and lowest in Chilko. Scale circulus counts of returning adult sockeye in their fourth year averaged 17.0 in Fraser, 14.6 in Cultus, 13.3 in Shuswap, and 12.7 in Chilko (Table 10). Based on estimates of relative duration of growing season between lakes, growth rate also appears to have been highest in Fraser, and as high in Chilko as in Cultus and Shuswap.

In calculating annual sockeye growth at Cultus, Shuswap, and Fraser, slower growing 2-yr-lake residents were not taken into consideration as numbers are small: fish with 2 yr in fresh water occasionally form up to 7% of brood smolt migrations (Cultus), or returning adults (Shuswap), and are not found among adults returning to Fraser. In Chilko, where 2-yr-olds are more numerous (up to 20% of each brood smolt population), weighted mean annual circulus counts were calculated from the circulus counts and percentage

age composition of 1- and 2-yr-olds produced. Weighted mean circulus counts of the 1949–68 broods averaged 0.4 circuli less than 1-yr lake residents (Table 10) with the value for individual years reduced by up to 1.0 circulus.

Comparison between mean smolt and adult circulus counts shown in Table 11 indicates that scale growth of returning adults accurately reflects that of smolts, and also reflects differences in smolt length and weight. The present comparison shows growth to the annulus to be almost identical, but as noted by Clutter and Whitesel (1956), adult scales exceed those of smolts by 0.6 in total circuli.

Factors Affecting Growth

The foregoing summary indicates a considerable range in rearing conditions found in four sockeye rearing lakes and a similar wide variation in sockeye abundance and growth. For two of the lakes (Shuswap and Chilko), for which sufficient concurrent data were available, multiple and partial correlation coefficients between certain of these factors and growth were calculated for a preliminary assessment of combined effects. The dependent variable was circulus count (logarithm) and the independent variables, although recognized as not

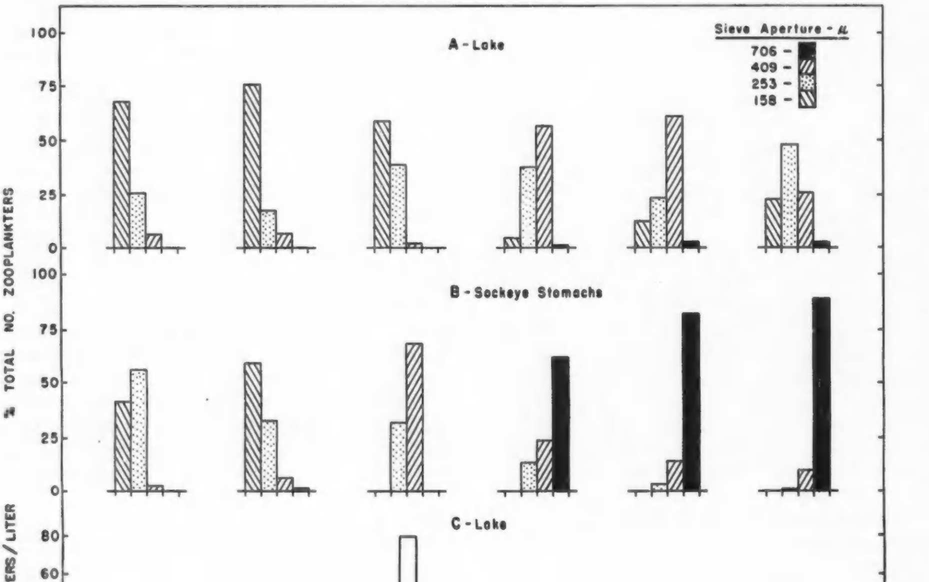


FIG. 4. Size composition and abundance of crustacean zooplankters in the lake and in sockeye fingerling stomachs (5 fish per sample) on the same dates, Fraser Lake, 1970. Percentage of stomach contents formed by insect pupae noted in (D). Onshore samples — April, May, June; midlake samples — August, October, November.

mutually exclusive, were sockeye density (logarithm), zooplankton standing crop, lake temperature (0–27 m), and temperature of the appropriate brood river during fry emergence and early lake residence (month of May). Multiple correlation coefficients for Shuswap and Chilko were 0.95 ($P < 0.01$) and 0.67 ($0.10 < P < 0.25$), respectively (Table 12). Examination of partial correlation coefficients indicated a high degree of association between sockeye density and growth at Shuswap, whereas at Chilko growth of sockeye appeared more closely associated with temperature. The association between sockeye growth and these factors — sockeye density, temperature, and zooplankton standing crop — are examined individually below.

TABLE 9. Sockeye electivity indices, Fraser Lake, 1970.

Date	706 μ	409 μ	253 μ	158 μ
Apr. 29	–	–0.4	+0.4	–0.3
May 18	–	0.0	+0.3	–0.1
June 5	–	+0.9	–0.1	–1.0
Aug. 27	+1.0	–0.4	–0.5	–1.0
Oct. 12	+1.0	–0.6	–0.8	–1.0
Nov. 14	+0.9	–0.4	–1.0	–1.0

DENSITY AND GROWTH

Within individual lakes, density and growth of sockeye are usually closely related. Increased density has been shown related to reduced growth of young sockeye in Babine, Dalnee, Cultus, and Owikeno lakes (as summarized by Johnson 1965), in Iliamna Lake (Mathisen and Kerns 1964) and in the Wood River lakes (Burgner 1964).

Increased density is also associated with reduced sockeye growth in most lakes used by Fraser sockeye, including at least three of the four lakes of the present study. Using parent spawners (females/ha) as an index of population density of the fry produced, and scale circulus count as a growth index, density-growth relations were examined for 20 annual spawning runs to each lake (Fig. 5). Correlation coefficients determined for the relation between

TABLE 10. Mean freshwater circulus count (spring growth omitted) and estimated growth rate from scales of adult sockeye with 1 yr lake residence in four lakes in the Fraser system.

	No. freshwater circuli 1949–1968 broods		Estimated average growth rate	
Lake	20-yr mean	Range of yearly means	No. circuli[a]	Circuli/week
Fraser	17.0	14.3–18.8	17.7	0.71
Cultus	14.6	10.2–18.3	18.6	0.52
Shuswap	13.3	10.5–17.0	12.4	0.41
Chilko	12.7	10.6–18.1	–	–
	12.3[b]	10.2–18.1[b]	12.4[b]	0.54[b]

[a]At lowest population density common to all lakes (3 females/ha).
[b]Weighted mean calculated from 1- and 2-yr lake residents — see text.

TABLE 11. Mean length, weight, and scale freshwater circulus counts of sockeye smolts from four lakes in the Fraser system. Circulus counts of adult sockeye of the same broods are included for comparison.

		Yearling smolts				Adults	
				Circuli		Circuli	
Lake	No. years	Fork length (*cm*)	Weight (*gm*)	To annulus	Total	To annulus	Total
Cultus	11	8.0	5.6	14.6	14.7	14.5	15.3
Chilko	20	7.8	4.6	12.6	13.2	12.7	13.8
Fraser	1	9.0	7.8	17.9	17.9	18.3	19.6
Shuswap	7	7.4	4.0	11.0	12.8	11.1	13.4

circulus count and density were increased for all lakes by partial logarithmic transformation (of density) but further logarithmic transformation of both circulus count and density increased the coefficient only at Shuswap, and here only slightly ($r = -0.930$ to $r = -0.945$).

In Cultus and Shuswap there is an inverse relation between density and growth, with correlation coefficients significant at the 1% level ($r = -0.778$ and r -0.930, respectively). Sockeye population density at Cultus Lake has been consistently higher than in the other lakes, with most spawning populations exceeding 8 females/ha. Growth decreased at densities over this level, dropping from 16 scale circuli at 10 females/ha to just over 10 circuli at 50 females/ha.

At Shuswap Lake, three separate levels of population density have occurred averaging approx-

TABLE 12. Correlation coefficients between circulus count and sockeye density, zooplankton standing crop, lake temperature (0–27 m), and May river temperature, in Shuswap and Chilko lakes.

	Shuswap Lake	Chilko Lake
Multiple correlation coefficient	0.945	0.670
Partial coefficient		
Sockeye density	-0.903	-0.300
Zooplankton	-0.055	0.186
Lake temperature	-0.079	-0.013
River temperature	-0.133	0.490
No. years	16	13

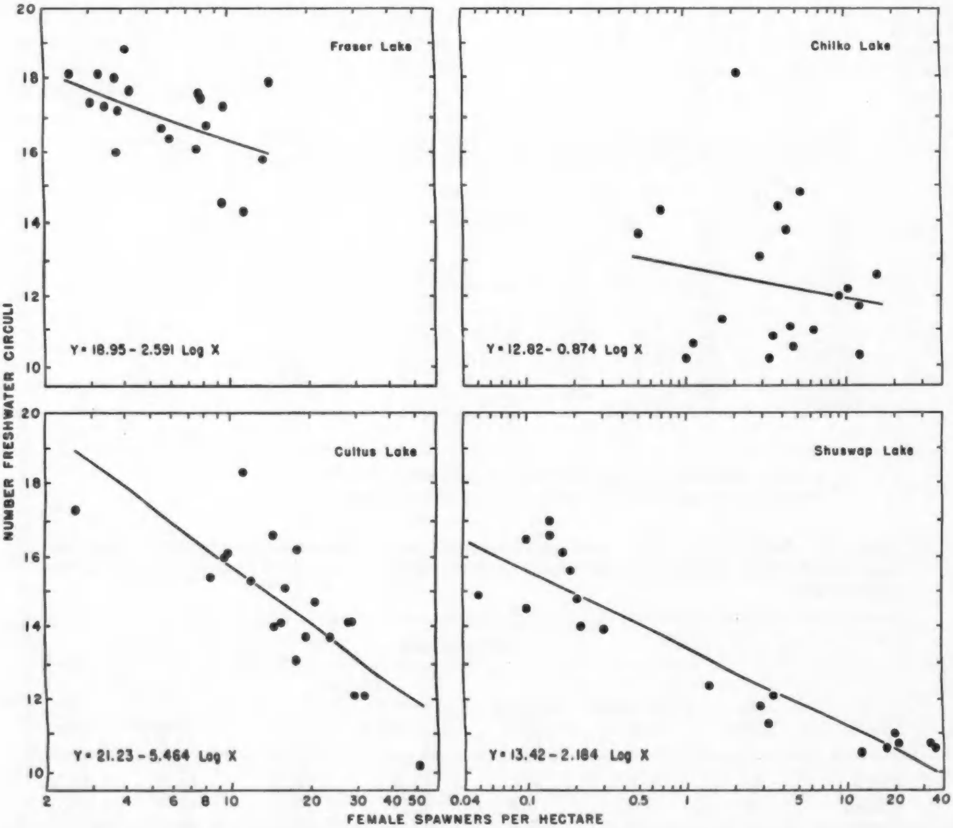


FIG. 5. Female spawners/ha of lake area and freshwater scale growth of offspring for 20 yr of spawning runs (1949–68) at Cultus, Chilko, Fraser, and Shuswap lakes.

imately 0.2, 3.0, and 23 females/ha. Growth declined from 15.6 to 11.9 circuli as densities increased from low to intermediate levels and at the highest density has averaged 10.7 circuli. At this high population density, growth has remained essentially constant over the range of densities recorded (12–36 females/ha). This levelling-off of growth at higher densities and the fact that logarithmic transformation of both data provided the closest correlation between density and growth suggests the relation is in the form of a negative exponential curve, as shown to describe sockeye growth in Iliamna Lake (Mathisen 1969).

Growth is also inversely related to density in Fraser Lake but, at least in the narrow range of densities tested (2–14 females/ha), the correlation coefficient was significant at only the 5% level ($r = -0.509$). Growth has been high, ranging from 14 to 19 circuli. At Chilko the only effect of increasing density appears to be the consistent low-to-moderate growth (< 13 circuli) when density has exceeded 9 females/ha, but at all lower densities growth has varied widely (10–18 circuli). This wide variation in growth does not appear to have been caused by undetected variations in fingerling density. Spawning populations at Chilko have provided an accurate index of subsequent smolt abundance, and the same wide range in growth is exhibited by all but the most numerous smolt populations.

Comparing growth between lakes at common theoretical population densities reveals a major difference between the two smaller lakes, Cultus and Fraser, and the two larger lakes, Chilko and Shuswap. In the range of population densities common to all lakes, approximately 3–14 females/ha, average growth has exceeded 14.0 circuli in Cultus and Fraser, but has averaged 12.5 circuli or less in Chilko and Shuswap. One factor influencing the density-growth relations is the size of the lake itself. Unless each fry population disperses throughout the entire lake (and this becomes progressively less likely as the distance from the point of fry entry increases) actual population density will be underestimated by the difference between the area available and the area inhabited. Johnson (1958) has shown that although population size influences fingerling dispersion in Babine Lake, even the largest populations use only a small part of the available nursery area.

Apart from the actual lake area utilized by the population, the rate of dispersion within the lake may also affect the density-growth relation. In large lake systems where large numbers of fry enter the lake from a single river, directional migrating behavior patterns appear to have evolved (Brannon 1972). However, even where distribution is deliberate, rate of fry movement (approx. 1 km/day) will limit availability of the total lake's food resources. In Shuswap Lake, for example, fry from Adams River are not dispersed throughout the Adams River arm until the end of July. Echo sounding in October 1971 showed an uneven distribution of fingerlings produced by the major 1970 spawning run (24 females/ha), with the greatest densities found near the Adams River spawning grounds and in the Salmon River arm of the lake, and lower densities in the Anstey and Seymour river arms. Similarly, even in relatively small Fraser Lake, sockeye fry were not uniformly distributed.

Although density-growth relations can be clearly demonstrated within at least three of the study lakes, density as examined here did not explain variability in growth within all lakes or account for all the differences in growth between lakes.

TEMPERATURE AND GROWTH

The influence of temperature on growth of sockeye has been demonstrated to be of major importance in laboratory studies (Brett et al. 1969; Brett 1971), but the influence of temperature and thermal structure under conditions of lake residence has not, as yet, been quantified. In the Shuswap system, fry migrating from Adams River inhabit both Shuswap and Little Shuswap farther downstream (Fig. 1). Because of high discharge of warm epilimnion water from Shuswap and rapid flushing and greater mixing in the small basin of Little Shuswap, temperatures to a depth of 15 m can reach 14 C by midsummer and the epilimnion remains cooler and deeper than in Shuswap. In contrast, marked stratification in the larger basin of Shuswap leads to temperatures of less than 9 C within a few meters of the surface. Under these conditions, by October 1972 sockeye fry reached a mean weight of 4.1 g in Little Shuswap but only 2.8 g in Shuswap. Zooplankton standing crops were similar in the two areas, and sockeye density was lower in Shuswap Lake.

Comparing the four study lakes, total growth attained at lowest densities has been greater in the three lakes (Cultus, Shuswap, Fraser) of warmest temperatures (mean 0–27 m over 9.5 C, see Table 3), and has frequently been lower and much more variable in the cooler temperatures (8.3 C) of Chilko. However, size and growth rate at a common density appear to have been as great in cooler Chilko as in Shuswap (Table 10), suggesting that lake temperature structure rather than average temperature per se may influence growth.

Although lake temperature is evidently associated with growth, little relation between year-to-year variations in lake temperature and growth fluctuations within a single lake could be demonstrated. Growth of Chilko sockeye compared with the May-to-October mean 0–27 m temperature over 14 yr showed a correlation coefficient of only $r = .45$ ($P < 0.25$). Sockeye growth in Shuswap Lake showed even less relationship to average lake temperatures. As sockeye density in Shuswap was shown to influence growth, years of intermediate and high density (> 1 female/ha) and low density (< 0.3 females/ha) were examined separately with the May-to-October mean 12–27 m temperature, considered representative of the depth of residence in this lake. Correlation coefficients for 8 yr at either density were not significant ($r = .37$ and $r = .39$, respectively, $P > 0.25$).

Relating growth and year-to-year lake temperature fluctuations clearly requires more detailed assessment of the lake temperature regime and of the distribution of juvenile sockeye within this varying thermal environment. In all four lakes, sockeye undergoing vertical feeding migrations would experience a range of temperatures during each 24-h period, as described for Babine Lake sockeye by Narver (1970). In assessing the effect of lake temperature on growth, the bioenergetic hypothesis (McLaren 1963; Brett 1971) may therefore be involved, wherein temperatures during both feeding and digestion of food may determine growth rate. In addition, the available food supply may dictate which temperature regime is most favorable for growth, because maximum food conversion efficiency is attained at progressively lower temperatures as food ration becomes more restricted (Brett et al. 1969).

Lake temperature structure has also been shown to influence fish movement. Young sockeye generally remain in the hypolimnion during thermal stratification, making short forays up through the thermocline to feed at the surface at dusk, as at Babine Lake (Narver 1970), or to areas primarily within the thermocline if surface temperatures are high, as in Lake Washington (Woodey 1972) and Great Central Lake (Barraclough and Robinson 1972). The latter situation may apply to Shuswap and Cultus lakes, where thermal stratification is marked and surface temperatures frequently exceed 20 C. Warm epilimnion and cold hypolimnion temperatures have been suggested to limit growth in Great Central Lake (LeBrasseur and Kennedy 1972), and evidence from the present study similarly suggests less growth occurs in stratified Shuswap than in Little Shuswap, where rapid flushing reduces surface temperatures and warms the hypolimnion.

Temperatures during fry emergence and early lake residence also differ between the four study areas. At least in the more northerly Chilko and Fraser lakes, where growing seasons are quite short, temperatures during this early period appear associated with yearly fluctuations in growth. At Chilko and Fraser, fry emergence begins at temperatures of 3.3 C (Brannon 1972) and lake temperatures during early lake residence warm slowly from 3–4 C in May to 6–8 C in June (Fig. 2). At Shuswap, fry emergence from Adams River begins at 4.4 C (Brannon 1972) and lake temperatures warm rapidly, at least near the surface, from 4 C in May to 14 C in June. Fry emerge from spring-fed beach areas in Cultus Lake (over an extended period from early April until late July, Brannon 1972) into lake temperatures, at the surface, of 5–16 C (Fig. 2).

To assess the effect of these early season temperatures on growth, mean temperatures of the incubation stream for the month of May (the period of peak emergence and early lake residence) were compared with sockeye growth (circulus counts) for all available years at Chilko, Fraser, and Shuswap. Cultus was omitted because dates of peak fry emergence into the lake are not monitored regularly. At Chilko, a positive association was evident between stream temperature and growth, with the correlation coefficient significant at the 1% level ($r = 0.716$). Circulus counts in years of high density (over 9 females/ha), which were omitted from the above analysis, tended to fall below the expected growth for a given temperature, indicating an influence of the higher population densities on Chilko sockeye growth. Inclusion of the years of maximum population density reduced the correlation coefficient to $r = 0.56$ ($P < .01$, 20 df).

Fraser sockeye growth and mean annual Stellako River temperatures for May were less closely associated. The correlation coefficient was significant only at the 5% level for population densities below 11 females/ha ($r = .52$) and reduced slightly ($r = 0.48$) with inclusion of all years. Growth of Shuswap sockeye and temperatures of Adams River during various periods surrounding fry emergence (April 15–May 15, May 1–31) showed no evident relation in years of either low or high sockeye density.

The degree of association between sockeye growth and early spring temperatures appears to be quite different for the three areas studied. Part of this dissimilarity may result from differences in the relation of incubation stream to nursery lake. Temperatures recorded in Chilko River reflect conditions in the rearing lake and those of Stellako River presumably influence conditions within the area of Fraser Lake first entered by the fry. In contrast, flow from Adams River enters the outlet region of Shuswap Lake (Fig. 1) with probably little influence on temperatures of the rearing area.

However, most of the difference between systems is believed to reflect the way temperature in these lakes is associated with growth. Growth of sockeye is a function both of temperature experienced and of length of time at which growth occurs. At Chilko Lake the growing season is the shortest among the lakes examined. Variation in length of the growing period and in initial rearing temperature should have the greatest influence on growth. Variation in lake heating during early spring at Chilko Lake would also have the greatest influence on the temperature regime throughout the short growing season, as May temperatures provide an index of subsequent lake temperatures ($r = 0.75$, $P < 0.01$, 12 df), at least in years of extreme variation from normal. At Fraser, growing season is slightly longer, with emergence timing and early spring conditions apparently having less impact on the total season's growth. At Shuswap, with a longer growing season, and with early spring temperatures less indicative of subsequent nursery conditions, the relation between growth and early spring temperature is not as close.

ZOOPLANKTON AND GROWTH

Interaction between juvenile sockeye and their primary food source has been studied by examining the effect of sockeye on zooplankton abundance, in terms of both total abundance and the particular zooplankters consumed, and then considering the relation between zooplankton and sockeye growth.

Reduction in zooplankton level attributed to grazing by large sockeye populations has been recorded in several lakes. Both at Cultus Lake (Ricker 1937b) and at Lake Dalnee (Krogius 1953), an inverse relation has been shown between the abundance of crustacean zooplankters in August (relative to the previous June) and the density of sockeye feeding in the lake. Johnson (1961) noted a progressive decrease in zooplankton standing crop of Babine Lake, with an increase in sockeye densities beyond 5000 fingerlings/ha. However, the reduction caused by grazing was considered of less importance in certain lake basins than that caused by rapid flushing rate (Johnson 1964). In Lake Aleknagik, one of the Wood River lakes, Alaska, "there has been an inverse linear relation ($r = -0.6$) between the standing crop of zooplankters and the grazing pressure exerted by the sockeye salmon fry during the last 10 years" (Mathisen 1972, from a report by D. E. Rogers 1971 personal communication). There is also a clear effect of grazing in Iliamna Lake, with reduced zooplankton levels 2 yr after the peak escapement during residence of the maximum biomass (mainly 2-yr-olds) of sockeye (Mathisen 1972). In contrast, Ruggles (1965) suggests that year-to-year fluctuations in Owikeno Lake zooplankton appeared to result from climatic fluctuation, and found no relation between zooplankton standing crop and juvenile sockeye abundance.

Effects of sockeye grazing on zooplankton standing crops were examined in the present study at the two lakes of long-term sampling, Chilko and Shuswap. For 14 yr at Chilko, zooplankton settled volume and sockeye density (females/ha) were not significantly correlated ($r = -0.33$) ($0.10 < P < 0.25$), although the general trend was inverse. Similar analysis for Shuswap over 19 yr produced an inverse relation which approached statistical significance at the 5% level ($r = -0.449$) ($0.05 < P < 0.10$).

To further assess the effect of sockeye grazing on zooplankton levels, Shuswap standing crops were compared with those in Mabel Lake, a 5870-ha lake draining into Shuswap through Lower Shuswap River (Fig. 1). Mabel has been used as a "control" lake for comparison with Shuswap, although it supports some kokanee (maximum spawning runs equivalent to 0.6 female sockeye/ha), and small sockeye runs (maximum 0.4 females/ha) coinciding with the years of maximum sockeye abundance in Shuswap.

Zooplankton levels at each location were examined and showed a significant decrease at Shuswap between years of low (< 0.3 females/ha) and intermediate (1–5 females/ha) sockeye density. A further small decrease in standing crop occurred in Shuswap in years of maximum sockeye densities (> 12 females/ha) (Table 13). Results indicate a reduction in zooplankton standing crop during years of intermediate and high sockeye density, particularly in the area near Adams River sockeye spawning grounds. Some reduction in standing crop also occurred in these same years throughout the system, including Mabel Lake. Possibly zooplankton standing crops are reduced by the sockeye and kokanee populations in Mabel, creating simultaneous fluctuations in standing crop throughout the system in some years. However, simultaneous wide variations in standing crop have also occurred in the two lakes in years of lowest sockeye density, possibly indicating some common climatic influence.

To assess the way sockeye predation may reduce zooplankton standing crops, sockeye feeding studies were examined. Sockeye feeding is most intense at dusk (Narver 1970), when sockeye migrate up toward the surface where many species of zooplankters are most concentrated. In lakes of moderate surface temperatures (Babine and Fraser) sockeye feed near the surface but in warmer lakes (Washington, Great Central) most fish feed at slightly greater depths (Woodey 1972; LeBrasseur and Kennedy 1972).

TABLE 13. Comparison of June–October mean zooplankton volumes (cm^3) in Shuswap and Mabel lakes at different levels of sockeye density in Shuswap Lake, 1955–1972.

Lake	Shuswap Lake sockeye density (females/*ha*)	No. years	Zooplankton (cm^3) mean (± 2 SD)	*t*
Shuswap Lake	<0.3	9[a]	1.29±.78	2.07(<.05)
	1.4–5.1	4[a]	.99±.34	0.16(NS)
	>12.2	6[a]	.93±.62	
Mabel Lake	<0.3	8	1.00±.50	1.21(NS)
	>12.2	5	.82±.12	

[a] Two stations sampled per year.

Studies at Fraser Lake indicated selective feeding by sockeye on the larger organisms present in the zooplankton standing crop. Selectivity of the largest zooplankters available (409 μ sieve) became evident when fry were still near shore in early June, and distinct selection of larger (706 μ sieve) organisms occurred later in the season after fingerlings had moved offshore. Similar size selectivity by feeding sockeye has been noted in Lake Washington (Woodey 1972), and in Cultus Lake where organisms of each species consumed by fingerlings were found to be of larger average size than those in the zooplankton standing crop (Ricker 1937b).

As suggested by Ricker (1937b), utilization of zooplankton food organisms by sockeye also appears related to mobility and habitat selection of the prey. Sockeye feeding studies at Cultus Lake (Ricker 1937b) indicated greater exploitation of Cladocera than of more mobile Copepoda of the same size. Results of Babine Lake feeding studies (Narver 1970) suggest greater utilization of *Daphnia* once sockeye ascended to the surface than of the larger or more abundant Copepoda (*Heterocope, Cyclops, Diaptomus*). Habitat selection of *Epischura* in the warm surface waters of Cultus Lake was suggested to reduce their exploitation by juvenile sockeye (Ricker 1937b), and similarly LeBrasseur and Kennedy (1972) suggested that warm surface temperatures reduced availability of zooplankton concentrations to feeding sockeye in Great Central Lake.

The highly selective feeding of sockeye should be reflected in the composition of the zooplankton. Most utilized species should be less abundant relative to less exploited ones, and differences in zooplankton size and species composition should be evident between lakes, as well as between years of high and low sockeye densities within one lake. This subject is presently being examined within several of the sockeye rearing lakes of the Fraser system. Analysis (Fig. 3) indicates not only a higher total standing crop, but a greater abundance of large zooplankters (706 μ sieve) in Fraser and Cultus than in Chilko, all in situations of low-to-moderate sockeye abundance (4.9, 5.1, and 1.6 females/ha, respectively). In less productive Chilko, few large organisms are present in the zooplankton, even in years of low sockeye density. The example presented for Shuswap is a year of maximum sockeye abundance (24 females/ha). Large zooplankters were not numerous and limited analysis suggests this proportion of large organisms was much reduced from years of lowest sockeye densities.

Growth of sockeye would then appear to be influenced in part by the abundance and availability of only certain organisms within the total zooplankton standing crop. Good growth of sockeye appears to occur in those situations where highly selective feeding can be carried out most efficiently. It is also possible that the greatest decrease in zooplankton standing crop and sockeye growth occurs as the larger organisms are progressively reduced to a low level of abundance, and sockeye must then begin to exploit a wider spectrum of the zooplankton. Once this has occurred, the relatively more numerous smaller zooplankters may be sufficiently abundant to maintain growth at this lower level without as marked a reduction occurring over a further increase in density.

An example of this situation may occur at Shuswap Lake, where reduction in zooplankton standing crop was found during years of high sockeye density. Zooplankton standing crop and sockeye growth decreased markedly as densities increased from 0.3 to 3 females/ha, but further decrease in zooplankton and growth was slight at densities up to 36 females/ha. At Chilko Lake a less pronounced effect of sockeye density on standing crop and sockeye growth was evident, possibly because the large zooplankters are never abundant in this very oligotrophic lake.

Summary

Each of the three factors examined — sockeye density, temperature, and zooplankton abundance — appear to be associated with somewhat different aspects of sockeye growth. In comparing lakes, the potential for growth seems associated with zooplankton abundance and availability, particularly of large organisms, and lake thermal structure and regime. Comparison of the four study lakes suggests that sockeye growth per hectare is greatest at Cultus and Fraser lakes, due to a combination of high zooplankton standing crop and somewhat different aspects of temperature. Cultus Lake becomes strongly stratified, which may not be conducive to rapid sockeye growth, but the long growing season appears to compensate for the low growth rate. The thermal structure at Fraser appears more favorable for sockeye growth, but the short growing season results in total smolt growth similar to that at Cultus. Shuswap has a lower zooplankton standing crop than does Cultus or Fraser and is also strongly stratified thermally, resulting in low growth despite a relatively long growing season. Chilko has a low standing crop of zooplankton, but an apparently favorable thermal structure. Growth rate is fast, but the short growing season limits total sockeye growth to approximately that of Shuswap.

Annual variation in sockeye growth is influenced by sockeye density within most lakes, but fluctuations in growth also appear associated with annual temperature variation. Variation in sockeye growth was associated mainly with sockeye density in the long growing seasons at Cultus and Shuswap. At Fraser, both density and temperature were associated with variations in growth, whereas in the short growing season at Chilko, most fluctuation in growth was associated with annual temperature variation. Density of fish was suggested to reduce sockeye growth through competition for a portion of the zooplankton standing crop.

Acknowledgments

The assistance of Dr G. Geen in reviewing the manuscript is gratefully acknowledged.

Collection of data and assistance from many members of the staff of the International Pacific Salmon Fisheries Commission have made this report possible.

ARMSTRONG, J. E. 1949. Fort St. James Map-Area, Cassiar and Coast Districts, British Columbia. Geol. Surv. Can. Mem. 252: 210 p.

BARRACLOUGH, W. E., AND D. ROBINSON. 1972. The fertilization of Great Central Lake. III. Effect of juvenile sockeye salmon. U.S. Fish Wildl. Serv. Fish. Bull. 70: 37–48.

BRANNON, E. L. 1972. Mechanisms controlling migration of sockeye salmon fry. Int. Pac. Salmon Fish. Comm. Bull. 21: 86 p.

BRETT, J. R. 1971. Energetic responses of salmon to temperature. A study of some thermal relations in the physiology and freshwater ecology of sockeye salmon (*Oncorhynchus nerka*). Am. Zool. 11: 99–113.

BRETT, J. R., J. E. SHELBOURN, AND C. T. SHOOP. 1969. Growth rate and body composition of fingerling sockeye salmon, *Oncorhynchus nerka*, in relation to temperature and ration size. J. Fish. Res. Board Can. 26: 2363–2394.

BURGNER, R. L. 1964. Factors influencing production of sockeye salmon (*Oncorhynchus nerka*) in lakes of southwestern Alaska. Verh. Int. Ver. Limnol. 15: 504–513.

CHAPMAN, J. D. 1952. The climate of British Columbia, p. 8–54. *In* Trans. 5th B.C. Nat. Resour. Conf.

CLUTTER, R. I., AND L. E. WHITESEL. 1956. Collection and interpretation of sockeye salmon scales. Int. Pac. Salmon Fish. Comm. Bull. 9: 159 p.

DALY, R. A. 1912. Geology of the North American Cordillera at the 49th parallel. Geol. Surv. Can. Mem. 38: 546 p.

1915. A geological reconnaissance between Golden and Kamloops, B.C. along the Canadian Pacific Railway. Geol. Surv. Can. Mem. 68: 260 p.

DAVIES, R. D. 1948. Geology in the mineral deposit of the eastern contact of the Coast Range batholith between Chilko and Whitesail lakes. Univ. British Columbia, Vancouver, B.C. 55 p. (unpublished thesis)

DAVIS, W. E., AND H. K. HILTZ. 1971. A constant-fraction sampling device for enumerating juvenile salmonids. Prog. Fish-Cult. 33: 180–183.

DEEVEY, E. S., AND G. B. DEEVEY. 1971. The American species of Eubosmina and Seligo (Crustacea, Cladocera). Limnol. Oceanogr. 16: 201–218.

EDMONDSON, W. T. [ed.] 1959. Fresh-water biology. John Wiley and Sons, New York, N.Y. 1248 p.

FOERSTER, R. E. 1925. Studies in the ecology of the sockeye salmon (*Oncorhynchus nerka*). Contrib. Can. Biol. 2: 335–422.

1929. An investigation of the life history and propagation of the sockeye salmon (*Oncorhynchus nerka*) at Cultus Lake, British Columbia. 1. Introduction and the run of 1925. J. Biol. Board Can. 5: 1–35.

1968. The sockeye salmon, *Oncorhynchus nerka*. Bull. Fish. Res. Board Can. 162: 422 p.

FOERSTER, R. E., AND W. E. RICKER. 1941. The effect of reduction of predaceous fish on survival of young sockeye salmon at Cultus Lake. J. Fish. Res. Board Can. 5: 315–336.

Hart, J. L. 1973. Pacific fishes of Canada. Bull. Fish. Res. Board Can. 180: 740 p.

Holland, S. S. 1964. Landforms of British Columbia, a physiographic outline. Bull. B.C. Dep. Mines Pet. Resour. 48: 138 p.

Howard, G. V. 1948. Problems in enumeration of populations of spawning sockeye salmon. Int. Pac. Salmon Fish. Comm. Bull. 2: 85 p.

International Pacific Salmon Fisheries Commission. 1950–73. Annu. Rep. 1949–72. Int. Pac. Salmon Fish. Comm. Annu. Rep.

Ivlev, V. S. 1961. Experimental ecology of the feeding of fishes. Yale Univ. Press, New Haven, Conn. 302 p.

Johnson, W. E. 1956. On the distribution of young sockeye salmon (*Oncorhynchus nerka*) in Babine and Nilkitkwa Lakes, B.C. J. Fish. Res. Board Can. 13: 695–708.

1958. Density and distribution of young sockeye salmon (*Oncorhynchus nerka*) throughout a multibasin lake system. J. Fish. Res. Board Can. 15: 961–982.

1961. Aspects of the ecology of a pelagic zooplankton-eating fish. Verh. Int. Ver. Limnol. 14: 727–731.

1964. Quantitative aspects of the pelagic, entomostracan zooplankton of a multibasin lake system over a 6-year period. Verh. Int. Ver. Limnol. 15: 727–734.

1965. On mechanisms of self-regulation of population abundance in *Oncorhynchus nerka*. Mitt. Int. Ver. Theor. Angew. Limnol. 13: 66–87. (Reprinted in Fish. Res. Board Can. (1965) Stud. 982(2): 66–87.

Killick, S. R. 1955. The chronological order of Fraser River sockeye salmon during migration, spawning and death. Int. Pac. Salmon Fish. Comm. Bull. 7: 95 p.

Killick, S. R., and W. A. Clemens. 1963. The age, sex ratio and size of Fraser River sockeye salmon, 1915 to 1960. Int. Pac. Salmon Fish. Comm. Bull. 14: 140 p.

Krogius, F. V. 1953. A contribution to the section on "Articles submitted for discussion" at the All-Union Conference on Problems of Fishery Management. Trudy Sovesch. Ikhtiol. Kom. Akad. Nauk SSSR 1: 218–223.

LeBrasseur, R. J., and O. D. Kennedy. 1972. The fertilization of Great Central Lake. II. Zooplankton standing stock. U.S. Fish Wildl. Serv. Fish. Bull. 70: 25–36.

Mathisen, O. A. 1969. Growth of sockeye salmon in relation to abundance in the Kvichak District, Bristol Bay, Alaska. Fiskeridir. Skr. Ser. Havunders. 15: 172–185.

1972. Biogenic enrichment of sockeye salmon lakes and stock productivity. Verh. Int. Ver. Limnol. 18: 1089–1095.

Mathisen, O. A., and O. E. Kerns Jr. 1964. Abundance, distribution, and size of juvenile red salmon of the 1960 year class in Iliamna Lake, Alaska, p. 191–202. *In* George Dahlgren [ed.] Proc. 14th Alaskan Science Conf. Am. Assoc. Adv. Sci. Alaska Div.

McLaren, I. A. 1963. Effects of temperature on growth of zooplankton, and the adaptive value of vertical migration. J. Fish. Res. Board Can. 20: 685–727.

Narver, D. W. 1970. Diel vertical movements and feeding of underyearling sockeye salmon and the limnetic zooplankton in Babine Lake, British Columbia. J. Fish. Res. Board Can. 27: 281–316.

Ricker, W. E. 1937a. Physical and chemical characteristics of Cultus Lake, British Columbia. J. Biol. Board Can. 3: 363–402.

1937b. The food and the food supply of sockeye salmon (*Oncorhynchus nerka* Walbaum) in Cultus Lake, British Columbia. J. Biol. Board Can. 3: 450–468.

1950. Cycle dominance among the Fraser sockeye. Ecology 31: 6–26.

1962. Comparison of ocean growth and mortality of sockeye salmon during their last two years. J. Fish. Res. Board Can. 19: 531–560.

Royal, L. A. 1953. The effects of regulatory selectivity on the productivity of Fraser River sockeye. Canadian Fish Culturist 14: 1–12.

Ruggles, C. P. 1965. Juvenile sockeye studies in Owikeno Lake, British Columbia. Canadian Fish Culturist 36: 3–21.

Ryder, R. A. 1965. A method for estimating the potential fish production of north-temperate lakes. Trans. Am. Fish. Soc. 94: 214–218.

Schaefer, M. B. 1951. A study of the spawning populations of sockeye salmon in the Harrison River system, with special reference to the problem of enumeration by means of marked members. Int. Pac. Salmon Fish. Comm. Bull. 2: 207 p.

Ward, F. J. 1957. Seasonal and annual changes in availability of the adult crustacean plankters of Shuswap Lake. Int. Pac. Salmon Fish. Comm. Prog. Rep. 3: 56 p.

Ward, F. J., and P. A. Larkin. 1964. Cyclic dominance in Adams River sockeye salmon. Int. Pac. Salmon Fish. Comm. Prog. Rep. 11: 116 p.

Ward, H. B., and G. C. Whipple. 1918. Freshwater biology. John Wiley and Sons, New York, N.Y. 1111 p.

Woodey, J. C. 1972. Distribution, feeding, and growth of juvenile sockeye salmon in Lake Washington. Ph.D. Thesis. Univ. Washington, Seattle, Wash. 174 p. + appendices.

Marion Lake (IBP) — from Bacteria to Fish[1,2]

KEN J. HALL

Westwater Research Centre
University of British Columbia, Vancouver, B.C.

AND KIM D. HYATT

Institute of Animal Resource Ecology
University of British Columbia, Vancouver, B.C.

HALL, K. J., AND K. D. HYATT. 1974. Marion Lake (IBP) — from bacteria to fish. J. Fish. Res. Board Can. 31: 893–911.

The microbial–detritus food chain in the sediment of Marion Lake, British Columbia, is an important pathway for the cycling of organic matter derived from both allochthonous (leaf litter) and autochthonous (phytoplankton, aquatic macrophytes, and benthic algae) sources. The activity of the sediment microbial community (approximately 10^9–10^{10} cells/g dry wt) as estimated by oxygen consumption and solute uptake is greatest during the summer months, when water temperatures are higher than 10 C. Solute uptake is also influenced by sediment depth, nutrient enrichment, sediment particle size, and oxygen concentration. Organic matter from natural sources such as algal excretion, interstitial water, and leaf detritus is complex and is not assimilated as rapidly as the simpler organic compounds.

Rainbow trout (*Salmo gairdneri*) and kokanee (*Oncorhynchus nerka*) in Marion Lake are characterized by small average size and slow growth rates. Fish production, although highly variable, is at the low end of the range compared to other salmonid producing systems. These characteristics are related to the inefficiency of trout and kokanee in cropping the benthic food supply. Experiments with individual predators and their prey have identified the nature of many of the interactions controlling the availability of benthic prey to the predators. Construction of simulation models shows promise as a means to quantify the importance of such interactions.

HALL, K. J., AND K. D. HYATT. 1974. Marion Lake (IBP) — from bacteria to fish. J. Fish. Res. Board Can. 31: 893–911.

La chaîne alimentaire microbienne–détritus dans le sédiment du lac Marion, Colombie-Britannique, est une voie importante pour le cyclage de la matière organique dérivée à la fois de sources allochtones (litière de feuilles) et de sources autochtones (phytoplancton, macrophytes aquatiques et algues benthiques). L'activité de la communauté microbienne du sédiment (environ 10^9–10^{10} cellules/g de poids sec), telle qu'estimée par la consommation d'oxygène et l'absorption des produits dissous, est à son maximum durant les mois d'été, alors que les températures de l'eau dépassent 10 C. L'absorption des produits dissous est aussi influencée par la profondeur du sédiment, l'enrichissement en substances nutritives, la grosseur des particules du sédiment et la teneur en oxygène. La matière organique provenant de sources naturelles, tels excrétion algale, eau interstitielle et détritus de feuilles, est complexe et n'est pas assimilée aussi rapidement que les composés organiques plus simples.

La truite arc-en-ciel (*Salmo gairdneri*) et le kokani (*Oncorhynchus nerka*) du lac Marion sont caractérisés par une taille moyenne petite et des taux de croissance lents. La production de poissons, bien que hautement variable, se situe à l'extrémité inférieure de la gamme, comparativement à celle d'autres régimes producteurs de salmonides. Ces caractéristiques sont liées à l'inefficacité de la truite et du kokani à récolter les ressources alimentaires du fond. Des expériences poursuivies avec des prédateurs individuels et leurs proies ont permis d'identifier la nature des nombreuses interactions contrôlant la disponibilité des proies benthiques à l'endroit des prédateurs. Des modèles simulateurs s'avèrent prometteurs comme moyen de quantifier l'importance de telles interactions.

Accepted December 10, 1973

[1,2] Footnotes, see page 894

Printed in Canada (J3247)

MARION Lake is located in the University Research Forest, at an elevation of 300 m on the south slope of the coastal mountains, approximately 50 km east of Vancouver, B.C. It is a small lake of 13 ha with a mean depth of 2.4 m. The climate is mild and wet with an annual precipitation of 240 cm/yr. This climate coupled with the impermeable substrata of the watershed and the morphometry of the basin, often result in rapid flushing of the lake (Efford 1967, 1969). As a result the water column communities are quite unstable with very low productivity, and the major energy flow appears to be through the benthic communities (Dickman 1969).

Marion Lake was selected as a site for a Canadian International Biological Program project, with the primary objective to determine the factors that control the rate of energy transfer between the major components of the ecosystem. To achieve this objective required determination of the size of the components and measurement of the major energy pathways between these components. Rather than attempt to summarize and integrate all the information collected on Marion Lake during this 10-yr study, two specific components of the study are discussed in some detail. These include, at the bottom of the food web, the microbial interactions and decomposition processes in the sediment and, at the top, the constraints on energy transfer in two populations of salmonids. Other aspects of the work on Marion Lake are described in the papers and theses listed at the end of this review.

Bacteria and Detritus

A recent symposium on the role of detritus in aquatic ecosystems (Melchiorri-Santolini and Hopton 1972) reemphasized the importance of the microbial–detrital complex (described by Odum and de la Cruz 1963) as being one of the major components of an aquatic ecosystem. After a preliminary investigation, it became apparent that the sediment-microbial community played an important role in the metabolism of Marion Lake through a detrital food chain (Efford 1969). To determine the energy sources that maintain this complex community, the factors which limit their production and size and activity of the microbial component became an important corollary to the study in order to achieve the initial objective of the program.

ENERGY SOURCES FOR MICROORGANISMS

The energy supply for microorganisms can be obtained from two basic sources, namely allochthonous input from the surrounding watershed and an autochthonous contribution from photosynthetic processes in the lake.

The inlet stream and the shoreline adjacent to the lake can be identified as sources of allochthonous material. G. H. Geen (unpublished data) investigated the input and output of dissolved and particulate organic matter in Marion Lake. He estimated that 467 g C/m^2 per year of dissolved and 50 g C/m^2 per year of particulate organic carbon (<1 mm diameter) entered the lake through Jacob's Creek. However, approximately 94% of the dissolved and 70% of the particulate fractions were lost through the outlet stream, making the food available from this source 33 g C/m^2 per year. Large detrital material that entered the lake, such as leaf litter and other plant fragments were monitored over a 6-mo period by W. E. Odum (unpublished data). In the inlet stream he found less than 10 kg dry weight of litter/week during the summer months, but values rose as high as 150 kg/wk in the autumn, due to accelerated leaf fall and heavy rains. He estimated that the carbon input from this source did not exceed 4 g C/m^2 per year. In addition to the inlet stream, there is leaf litter input from the eulittoral zone which is covered with sedges, the small shrub *Myrica gale*, and other shrubs and small trees such as salmonberry (*Rubus spectabilis*) and alder (*Alnus rubra*). Periodic flushing of this zone by high lake levels during the fall rains help to transport this material into the lake. Through estimation of the vegetation zones by aerial photography and surface mapping, and from production estimates, Odum estimated an input of 17 g C/m^2 per year.

Chemical analysis of leaf litter and lake sediments (Table 1) demonstrated a gradual change in

TABLE 1. Chemical composition of leaf litter and sediment (as percent dry weight).

Description	Carbohydrate	Protein	Tannins	Organic matter
Salmonberry (fresh, labelled)	25.0	20.6	–	95.6
Sweet gale (fresh, labelled)	24.4	21.4	5.7	95.2
Dead litter (forest floor)	15.5	27.3	6.1	86.7
Dead litter (from lake sediment)	10.9	38.2	5.2	91.0
Lake sediment (average for 1 and 4.5 m samples)	5.3	10.9	2.5	37.6

---

[1]This paper, part of a special issue that comprises a comprehensive review of Limnology in Canada, was prepared to mark the 19th Congress of the International Association of Limnology (SIL), in Winnipeg, Man., during August 1974.

[2]Canadian Contribution to the International Biological Program No. 254.

the chemical composition of the leaf litter as it was washed into the lake and processed by aquatic organisms to become a stable component of the deeper lake sediments (Hall et al. 1973). There was a gradual decrease in the carbohydrate as the leaves were processed and the protein content of the litter increased, probably as a result of colonization by the lake microorganisms. Kaushik and Hynes (1971) observed a similar trend in a study of leaf decomposition in Ontario streams. Both carbohydrate and protein content decreased as the leaves became a stable component of the sediment, attributable partially to dilution with mineral materials, as the carbon content of the sediment decreases to one-third the value of the leaf litter.

The carbon input through in situ photosynthesis has been summarized by Efford (1967). The contribution by phytoplankton was small, namely 8 g C/m^2 per year. The main reason for the low productivity of this component was attributed to the high flushing rate of the lake. With heavy rainfall, it was not unusual for the lake to exchange its water volume in less than 2 days. Estimates of primary productivity of the benthic algae made by Hargrave (1969b) and Gruendling (1971) were 40.4 and 44.2 g C/m^2 per year, respectively. The most important variables influencing productivity in this community were temperature, algal standing crop, and light. Primary productivity was highest during the summer months, and the largest total standing crop occurred at 2 m (Gruendling 1971). This was attributed to light limitation in the deeper waters (3–4 m) and grazing pressure in the shallow waters (0.5–1 m). Aquatic macrophyte production estimated by ^{14}C uptake and organic matter changes was 18 g C/m^2 per year (Davies 1970). This production occurred from May through August and was distributed in only 20% of the lake. Thus, there is an apparent input of 68 g C/m^2 per year due to primary productivity in the lake. Some of this organic matter is consumed directly by zooplankton, benthic invertebrates, and tadpoles. The rest is available for degradation by microorganisms and can be cycled to the higher trophic levels through a microbial-detritus complex. The primary sources of carbon available in Marion Lake are summarized below.

	g C/m²/yr
Dissolved carbon (Inlet–outlet stream)	28
Particulate carbon <1mm (Inlet–outlet stream)	15
Particulate carbon > 1 mm (mainly leaf litter)	4
Leaf litter (eulittoral zone)	17
Phytoplankton	8
Benthic algae	42
Aquatic macrophytes	18

ENUMERATION OF MICROORGANISMS IN SEDIMENT

Determination of the numbers of bacteria in sediments has posed a difficult problem to microbial ecologists for many years. Several techniques have been reviewed by Rodina (1972) and Sorokin and Kadota (1972), but they rarely determine accurately the total numbers present. Plate counts usually underestimate the bacteria as there is no universal medium on which they can all be cultured. Direct counts are difficult and often not accurate, as it is often impossible to segregate bacteria from sediment particles or distinguish them from some of the microalgae.

Several attempts have been made to estimate the biomass of bacteria in the sediments of Marion Lake. P. M. Fraker (unpublished data) found that sediment dilutions plated on nutrient agar containing 0.5% yeast extract gave the greatest number of colonies. There was a seasonal fluctuation in the numbers, with a peak of 2×10^6 cells/cm^3 in midsummer and 5×10^4 cells/cm^3 in midwinter. Unfortunately this technique did not count most of the bacteria on the inside of aggregates of sediment particles not adequately dispersed in the plating technique. Ramey (1972) used a number of direct count techniques, including bright field and fluorescence techniques, and found bacterial numbers of 10^8 cells/g dry wt of sediment. The predominant organism appeared to be a small particle-associated coccoid, with greatest density at a 2-cm depth. A modified membrane filtration technique has been used by B. K. Burnison (unpublished data) for direct counts of sediment bacteria. The bacteria are stained with fluorescein isothiocyanate and counted by fluorescence microscopy. Figure 1 gives a depth profile of bacteria numbers in the top 6 cm of the lake sediment. There is a gradual decrease in bacteria with depth in contrast to the 2-cm maximum reported by Ramey (1972). The values are at least two orders of magnitude larger than the plating values reported by Fraker. Assuming a cell volume of 0.36 μ^3 and using direct counting techniques, this gives a bacterial biomass of 3.9 mg bacteria/g dry wt of surface sediment during June.

The measurement of adenosine triphosphate (ATP) has been utilized by several investigators as a measure of the microbial biomass in the aquatic environment (Holm-Hansen and Booth 1966; Lee et al. 1971). A difficulty in utilizing ATP measurements is that all live organisms contain ATP and must be separated from the bacteria or their bio-

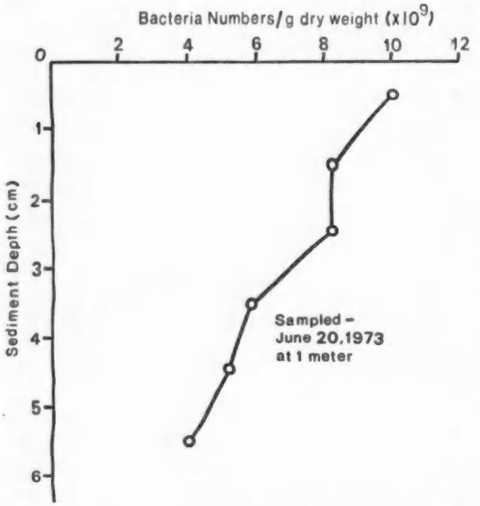


FIG. 1. Vertical profile of sediment bacteria.

mass determined and a correction made to eliminate their ATP contribution. From measurement of ATP in the sediment, E. Perry (unpublished data) estimated the total sediment biomass at 7.13 ± 0.74 mg/g dry wt with 1.99 ± 0.2 mg/g dry wt (28%) being contributed by bacteria and microalgae. This value is within 50% of the value obtained by Burnison using direct counts, so the range in size of bacterial component by two independent techniques appears to be 2–4 mg/g dry wt in surface sediment.

Fungi form an important component of the microbial sediment community. Many groups of fungi possess exocellular enzymes capable of degrading very resistant materials, such as humic substances and insect exuviae, and, therefore, play an important role in the cycling of organic matter. Dick (1971) studied the occurrence and distribution of saprophytic fungi in Marion Lake sediments. He concluded that the marginal sediments were richer in fungi and suggested many fungi recorded in the lake sediments were from alien spores which originated from the emergent littoral flora. C.-Y. Chang (unpublished data) estimated the numbers of viable fungal propagules and reported values ranging from 17.6×10^3 to 81.6×10^3/g dry wt of sediment.

In contrast to Dick (1971) Chang found higher numbers in deeper sediments. Vertical distribution in the sediments showed a trend similar to numbers of bacteria (Fig. 1). The surface sediments (0–1.5 cm) contained 32.7 to 54.0×10^3 propagules/g sediment while the section from 1.5 to 3 cm contained only 10.0 to 14.7×10^3 propagules/g sediment. Compared to numbers of bacteria, the fungi appear to be relatively unimportant. However, a number or biomass comparison may not be significant, because the activity and special degradative abilities of the fungi may be of greater importance in energy transfer in the lake ecosystem.

Activity of microorganisms — When it became apparent that the benthic bacteria were a major component in cycling energy in sediments of the lake, measurement of this activity and the factors which control it became important. Due to the complex nature of the bacteria and the associated sediment community, it was necessary to design simple assays that would give an estimate of their activity.

Hargrave (1969b) used differences in oxygen uptake in sealed sediment cores in the presence and absence of antibiotics to separate the bacterial component of total community respiration. He concluded that bacteria accounted for 30% of the oxygen consumed by the sediment community and this proportion increased to a maximum of 45% in the winter months. It has been demonstrated recently that antibiotics do not kill all the bacteria and that respiration may be stimulated by antibiotics, which apparently eliminate competition and allow accelerated activity of some of the resistant species (Cameron 1973). Also, since oxygen is depleted 1 cm below the sediment surface (Hargrave 1970) a good portion of the microbial population is facultative or anaerobic, and their metabolic activity will not be measured by oxygen consumption.

An attempt has been made to estimate the "bacterial biochemical potential" of the benthic bacteria in Marion Lake (P. M. Fraker, unpublished data). Using plating techniques, she isolated 20 types of bacteria which represented 86% of the total plate count. These types were arbitrarily characterized by colony color, size, elevation, edge characteristics, and soluble pigment. A seasonal study was made of the ability of the 20 types to utilize the solutes glycine, glucose, xylose, lactic acid, acetate, and cysteine as sole sources of carbon. The response to potential sources of these materials was then correlated. There was no clear seasonal response for utilization of all substrates. For example, the percent of the population that could utilize glycine was highest during winter months, whereas acetate and cysteine utilization were more prominent during spring and summer. Correlation of the microbial potential with possible chemical sources (primary productivity and detrital inputs) were not significant, probably due to a slow release of the substrates from the materials being degraded.

The assimilation dynamics of soluble organic compounds by sediment bacteria has been studied with radioactive tracers, in an attempt to estimate the importance of the complex bacterial sediment community and determine the transfer rates between the pool of dissolved organic matter and the heterotrophic community (Hall et al. 1972). Measurement of the maximum uptake rate of three radioactive organic substrates (glucose, glycine, and acetate) demonstrated a seasonal fluctuation, with the greatest activity occurring during the summer months when water temperatures were above 10 C (Fig. 2). Although temperature influenced the seasonal response, other factors had some influence on the uptake rate and turnover time for these organic compounds. There was a decrease in the uptake rate of glucose and acetate by sediment at 3 cm when compared to surface sediment. This decrease in activity compared favorably with the decrease in bacteria numbers determined by Burnison. The segregation of sediment particles caused an increase in the uptake rate of glucose at higher temperatures, indicating that diffusional processes were probably exerting some control over uptake, especially when activity was greater. Nutrient enrichment (N/P inorganic fertilizer) in isolated enclosures in the lake caused an increase in the maximum uptake rate for glucose and could be of some importance in controlling activity in the nutrient-poor waters of Marion Lake. In mixed sediments, anoxic conditions did not affect the uptake rate of glucose, but in undisturbed sediment cores the uptake under anoxic conditions decreased by as much as 30–50% (K. J. Hall et al. unpublished data). The different response of the two systems to oxygen was possibly attributed to the fact that mainly aerobic organisms were contacted in the undisturbed sediment, but in mixed sediments (top 3 cm of a core) the solute would contact both aerobic and facultative organisms which were not affected as much by oxygen depletion.

To determine the assimilation efficiency of the organic compound, it was necessary to measure the amounts mineralized ($^{14}CO_2$ respired). All three solutes were mineralized during the incubation period. Figure 3 shows the seasonal variation in mineralization rates for undisturbed cores inoculated with 50 µg/liter of solute. There was also a difference in percentage of solute that was mineralized. This percentage was not consistent with different sediment treatments (mixed or undisturbed) and showed some seasonal fluctuation, especially in the undisturbed cores.

	Mixed		Undisturbed	
Solute	avg % mineralized	range % mineralized	avg % mineralized	range % mineralized
Glucose	22	18–31	28	15–56
Glycine	63	45–87	45	24–75
Acetate	13	9–16	40	16–70

All isotopes demonstrated the same seasonal oscillation in percent mineralization in undisturbed sediments, suggesting that changes in the assimilation efficiencies of the heterotrophic community could be due to seasonal changes in the predominant bacteria that constituted the sediment microflora.

The three solutes studied comprise only a small percentage of the dissolved organic matter released

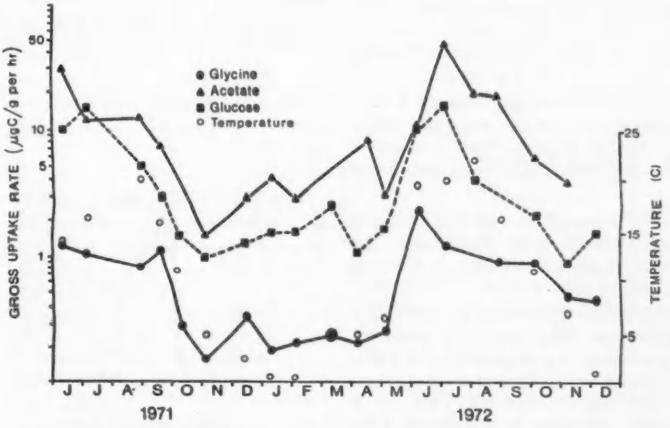


FIG. 2. Seasonal variation in gross uptake rates for mixed sediments.

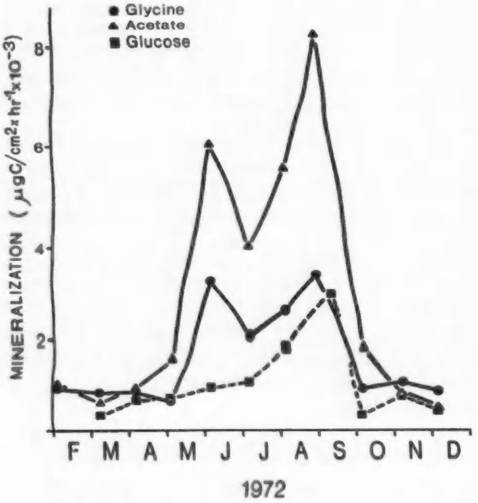


FIG. 3. Seasonal mineralization rates for undisturbed cores.

by hydrolytic enzymes during decomposition processes and made available for assimilation by sediment bacteria. Inhibition studies demonstrated that a common transport mechanism did not exist for other solutes of similar structure, indicating that uptake mechanisms were complex and could not be completely described by a study with only three solutes.

UTILIZATION OF NATURAL SUBSTRATES

Although the assimilation of simple organic compounds provides an estimate of the relative activity of a microbial community, most of the material available to microorganisms is more complex and the utilization rate per mole of carbon is certainly much slower. To be more representative of the types of compounds available to the benthic microorganisms, several studies were conducted to determine the flux of "naturally" produced materials.

Algal excretion products — To investigate the possible significance of algal excretion products as a source of dissolved organic matter in sediments, Kleiber (1972) conducted experiments with ^{14}C-bicarbonate in light and dark sediment cores to determine excretion rates. Rapid turnover of some of the organic compounds by bacteria caused problems in determining algal excretion rates, as it created an apparent decrease in excretion with increasing incubation time.

By extrapolation to zero time in several experiments, the proportion of the algal photosynthate excreted was found to vary between 0.038 and 0.22. The higher value coupled with primary productivity estimates by Hargrave (1969b), provided an estimate of the carbon flux as high as 8.8 g C/m² per yr to the interstitial dissolved organic matter pool. Comparing the excretion values to uptake estimates for the same period (Hall et al. 1972), it was apparent that natural algal excretion was of relatively minor importance to the heterotrophic community except possibly for bacteria closely associated with the benthic algae.

G. G. Marten (unpublished data) estimated the turnover of the dissolved organic matter excreted by the benthic algae by injecting labelled excretion products into the top centimeter of fresh undisturbed cores and monitoring the activity remaining in the interstitial water. The drop in activity was exponential and gave an estimated turnover rate of 0.5 h. A dialyzed fraction of low molecular weight had the same turnover time. Only 10% of the total activity remained in the interstitial water after 24 h. In another experiment, the molecular size characteristics of an algal exudate and the fractions that were physically adsorbed actively taken up by the sediment microorganisms were studied (K. J. Hall, unpublished data). The molecular size distribution of a ^{14}C-labelled algal exudate separated on Sephadex G-25 demonstrated that 43% had a molecular size of 5000 or larger (Fig. 4). Uptake experiments with the total algal exudate followed by gel filtration of the fraction remaining in solution demonstrated that 34.5% of the exudate was physically adsorbed by dead sediment and 46.5 % removed by an active sediment. Physical adsorption removed both high and low molecular weight components, whereas active uptake removed an additional 12% mainly from the low molecular

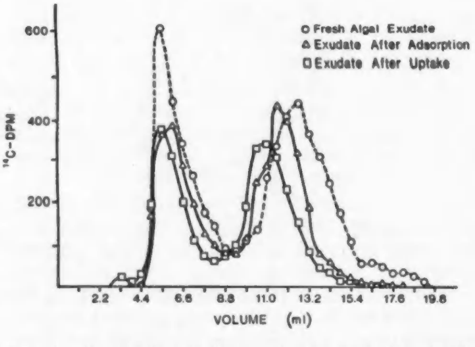


FIG. 4. Separation of algal exudate on Sephadex G-25.

weight component. The large differences in the percent of the algal exudate remaining in solution in the two studies could possibly be attributable to the differences in sediment treatments since mixed sediments were used in the molecular size study and undisturbed cores in the other. Also, differences in the physiological state of the algae could produce an exudate with different uptake characteristics.

Interstitial dissolved organic matter — The excretion products of the benthic algae form only a fraction of the organic compounds in the interstitial water that are available for microbial assimilation. To determine the importance to the microorganisms of the dissolved organic fraction in the interstitial water, a mixed bacterial culture isolated from the sediment (Bae et al. 1972) was placed in a chamber (Gaswami and Green 1971). Changes in the concentration of dissolved organic carbon were measured to determine the fraction available to the bacteria (Fig. 5). They were capable of utilizing 50% of the organic matter, and the system became stable after 10 days (B. K. Burnison, unpublished data). Continual recycling of some of the organic matter through the production and decomposition pathways of the bacteria during the experimental period (20 days) could complicate interpretation of this experiment. However, the region of stabilization indicated that at least half of this organic matter was inert to microbial attack.

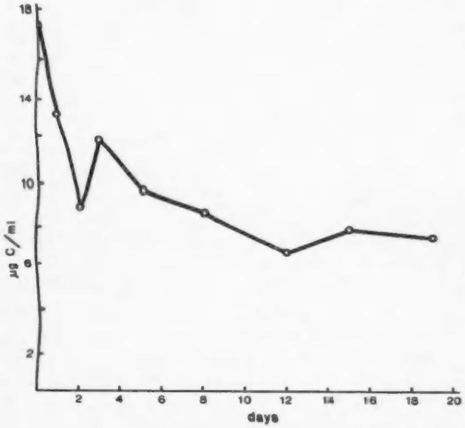


FIG. 5. Depletion of dissolved organic matter in interstitial water by sediment bacteria.

In other experiments, radioactive dissolved organic matter was prepared by incubating sediment with glucose for 1 wk and then recovering the labelled interstitial fraction (G. G. Marten unpublished data). This material was injected into fresh undisturbed cores and gave a turnover of 0.78 h^{-1}. Twenty-five percent of the labelled material was adsorbed immediately and 30% still remained in the interstitial water after 24 h. This material had a much faster turnover rate than the natural material isolated by Burnison, but this labelled dissolved organic matter probably did not contain the humic fractions which accumulate in the dissolved organic matter of interstitial water and are resistant to microbial action.

Utilization of leaf detritus — W. E. Odum (unpublished data) found that leaf litter was an important component in the carbon budget of Marion Lake. To determine the assimilation dynamics of leaf litter, continuous flowing sediment microcosms containing radioactive leaf litter were set up and the labelled carbon dioxide and dissolved organic matter monitored (Hall et al. 1973). Monthly samples were taken from the microcosm to determine residual activity and changes in leaf quality. Typical results are summarized in Tables 2 and 3. As much as one third of the total activity was respired in a

TABLE 2. Partitioning of radioactivity in sediment microcosms.[a]

Sample	Experiment duration	Leaf litter recovered	Percent activity in			
			a) Leaf litter	b) CO_2	c) Released DOM	d) Particles[b] <1mm
Salmonberry	1 month (May 11–June 15)	63.5	26.4	18.1	10.1	45.4
Salmonberry	2 months (July 1–Sept. 1)	28.3	1.8	16.0	5.8	76.4
Sweet Gale	3 months (Sept. 2–Nov. 30)	31.3	10.8	33.0	15.4	40.8

[a] Average values for duplicate microcosms.
[b] Calculated by difference.

3-mo period (10% of the total occurring during the first 10 days). Significant amounts of labelled dissolved organic matter were released during the early stages of decomposition but decreased rapidly, presumably due to the colonization of the leaf litter by sediment microorganisms. Oxygen consumption measured by a microwinkler procedure was as high as 10 mg O_2/day during the first 3 wk, but decreased to 4 mg O_2/day near the end of the experiment. Between 40 and 75% of the activity was incorporated into the sediment or degraded to fragments <1 mm in size. This variability was dependent on the type of leaf litter and the sediment activity.

SUMMARY

The information concerning the bacteria-dissolved organic carbon (DOC) — particulate organic carbon (POC) food chain is difficult to summarize due to its complexity and the many factors that can influence the size of the components and the transfer rates between them. Figure 6 is an attempt to summarize some of this data. It presents the sediment bacteria and the detrital POC as separate components, but the true nature of the system is probably a microbial–detrital complex which is grazed continuously to remove the bacteria that grow on the organically rich detritus until it becomes a reasonably stable component of the sediment.

TABLE 3. Change in chemical quality of sweet gale in microcosm.

Time	Carbohydrate	Protein	Organic matter
Initial	24.4	21.4	95.2
30 days	16.9	34.0	89.9
60 days	15.2	34.1	83.0
90 days	15.6	35.8	84.5

Many of the transfer rates between compartments have not been determined. For example, a large proportion of the organic matter of phytoplankton, aquatic macrophytes, and benthic algae is cycled through the POC and bacterial compartments before being incorporated into the higher trophic levels such as amphipods and insect larvae. Considerable research is still necessary to determine the proportions of these components utilized directly by grazers and through the detrital food chain.

Several assumptions have been made in calculating many of the transfer rates. It has been assumed that the decomposition rates of leaf litter entering the lake are similar to rates found for radioactive leaves in sediment microcosms. Also, the utilization rate of interstitial DOC has been calculated on the basis of uptake kinetics for only three low molecular weight compounds, but it is evident that many more substrates are present in interstitial water and that some have slow assimilation rates as was demonstrated by the uptake of algal excretion products and interstitial DOC. Many of the transfer rates are presented as a range of values, in an attempt to indicate the variability observed under the different environmental and experimental conditions employed.

The metabolism of Marion Lake is focused around the sediment community, which receives organic matter from both allochthonous sources and primary production in the lake. This component of the study has provided information on the size

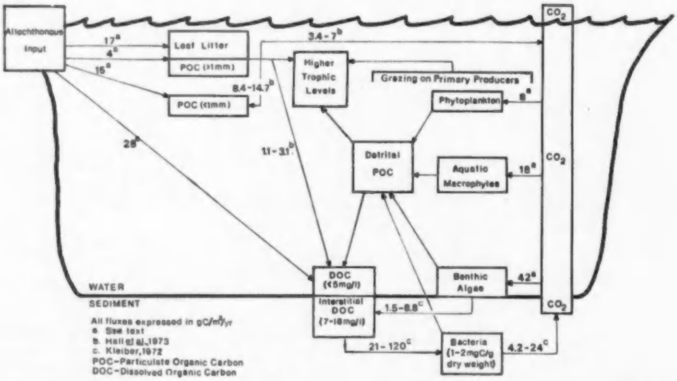

Allochthonous Input
17a
4a
15a
28a
Leaf Litter
POC (>1mm)
POC (<1mm)
3.4-7b
8.4-14.7b
1.1-3.1b
Higher Trophic Levels
Grazing on Primary Producers
Phytoplankton
8a
Detrital POC
Aquatic Macrophytes
18a
CO2
CO2
CO2
DOC (<5mg/l)
Benthic Algae
42a
WATER
SEDIMENT
Interstitial DOC (7-18mg/l)
1.5-8.8c
21-120c
Bacteria (1-2mgC/g dry weight)
4.2-24c
All fluxes expressed in gC/m²/yr
a. See text
b. Hall et al.,1973
c. Kleiber,1972
POC-Particulate Organic Carbon
DOC-Dissolved Organic Carbon

FIG. 6. Diagrammatic representation of dissolved organic matter and detrital food web in Marion Lake.

of the microbial component, its activity, and many of the factors which exert some control over this activity. The complexity of the bacterial–detritus system has become more evident through this study and poses several interesting areas for future research.

Population Characteristics of Salmonid Fishes in Marion Lake and Constraints on Energy Transfer to Them

One of the primary aims of the projects in freshwater ecology sponsored by IBP was to calculate the production of fish in a particular body of water. However, Backiel and LeCren (1967) suggested that production estimates should only be a means to the understanding of the freshwater ecosystem of which fish are a part, and that a second goal is to concentrate on elucidating the factors that control the rate of energy flow through an ecosystem and specifically those trophic levels represented by fish. Finally it is desirable to integrate information about the factors controlling the rate of energy flow to produce either conceptual or mathematical models which allow us to make predictions about the current ecosystem as well as about the consequences to vertebrate predators of selective changes in the ecosystem.

The research on fish populations in Marion Lake has passed through all the above-mentioned phases, although particular aspects have received more attention than others. This section is an attempt to trace the work from description of fundamental population characteristics (e.g. numbers, biomass, growth, production, etc.) to experimental determination of constraints on energy transfer between fish and their prey, and finally to the formulation of some deterministic models of predator feeding.

POPULATION CHARACTERISTICS

Rainbow trout (*Salmo gairdneri*) and landlocked kokanee (*Oncorhynchus nerka*) are the species of fish that inhabit Marion Lake. They may have invaded the lake after the last glaciation approximately 12,700 yr ago (Mathewes 1973), or have been planted in the early 1900s (I. E. Efford personal communication). Regardless of their origin, the two species constitute self-sustaining populations and complete their life cycle within the confines of the lake and the few miles of stream not blocked by waterfalls.

Population estimates of trout and kokanee age 1+ and older in 1963 (Sandercock 1969) and in 1972 (K. Hyatt unpublished data) indicate a range of total numbers between 3600 and 13,000 fish (263–977 fish/hectare). The wide variation is due primarily to the calculation of the number of kokanee present (Table 4). In both instances the population estimate of kokanee was calculated by assuming a ratio of kokanee to rainbow trout in the lake. The numbers of trout estimated by mark recapture techniques on both occasions appear to be more stable. The variability in kokanee numbers (150–690/hectare) is not entirely unexpected; Johnson (1965) reported that over an 8-yr period in the Babine–Nilkitkwa lake system lake densities of sockeye juveniles (taxonomically indistinguishable from kokanee) ranged from less than 150 to greater than 90,000 fish/hectare.

Different patterns of reproduction constitute another reason for predicting relative variability in kokanee population size as compared to trout. Kokanee, as with all members of the genus *Oncorhynchus*, spawn only once and then die. In Marion Lake kokanee spawn at age 2+ or 3+ (Table 5). Trout have a more flexible reproductive

TABLE 4. Estimates of population size and age-class structure.

Salmonid	Kind of estimate	Data source	Population size	% in each age-class 1+	2+	3+	4+
Trout	Modified Schnabel	Sandercock (1969)	3977	56.3	34.6	8.7	.4
	Petersen	Hyatt (unpublished data)	2000	58.5	30.0	9.0	2.3
Kokanee	Ratio of kokanee to trout 2.25:1	Sandercock (1969)	9000	58	37	5	–
	Ratio of kokanee to trout 1:1.25	Hyatt (unpublished data)	1600	–	–	–	–

TABLE 5. Percentage of fish reaching maturity at each age (Sandercock 1969).

Parameter	Trout								Kokanee					
Age at	1+		2+		3+		4+		1+		2+		3+	
spawning	M	F	M	F	M	F	M	F	M	F	M	F	M	F
% mature	0	0	36.7	0	44.7	72.9	100	100	0	0	62	72	100	100

pattern and may spawn several times; this means that the spawning population is made up of a number of year-classes which in turn produce a stability in overall population abundance not attainable by kokanee.

Reproduction of rainbow trout in Marion Lake occurs in mid-April and of kokanee in mid-October. This major event in the life histories of the two species is reflected in the changes in energy content of the fish throughout the seasons (Fig. 7). Large amounts of energy are evidently mobilized at appropriate times of the year to carry out the reproductive effort.

Sandercock (1969) calculated the fork-length fecundity relationships of trout ($F = 18.7\ L^{0.959}$) and kokanee ($F = 2.84\ L^{1.414}$). He estimated the total egg deposition and fry survival to time of lake recruitment based on a population of 4000 trout and 9000 kokanee and the size-class structures of the populations in 1963–64 as follows:

	Trout	Kokanee
Total no. eggs	124,000	140,000
Avg no. fry	2,350	6,850
Survival to recruitment	1.9%	4.9%

His estimate seems reasonable for rainbow trout; observations of juvenile recruitment to the lake during July–September 1972 (K. Hyatt, unpublished data) indicated the entry of 1000 recruits based on a lake population of 2000 trout 1+ and older. There are no direct observations of kokanee recruitment to the lake. Low egg-to-fry survival rates in Marion Lake are expected in view of a restricted area available for spawning and highly variable water-flow rates which occur while eggs and fry are in the gravel (Sandercock 1969).

Appreciable growth by trout occurs during both stream and lake residence. Juvenile trout ordinarily spend the first 2–3 mo of life in the inlet stream of Marion Lake, and their growth during this period approximates that of trout in other British Columbia watersheds (K. Hyatt unpublished data). They recruit to the lake after reaching a total length of 4–5 cm. It is assumed that kokanee enter the lake shortly after emerging from the gravel, so that all appreciable growth takes place in the lake.

In Marion Lake, trout and kokanee are characterized by small, average adult size (trout 17.5 cm, kokanee 14.0 cm). The size of fish in a population depends on factors which affect both the average age and the growth rate (LeCren 1958). Efford (1969) compared the length–age relationships of rainbow trout in Marion Lake with comparable information from a large number of other lakes in British Columbia (Larkin et al. 1956) and concluded

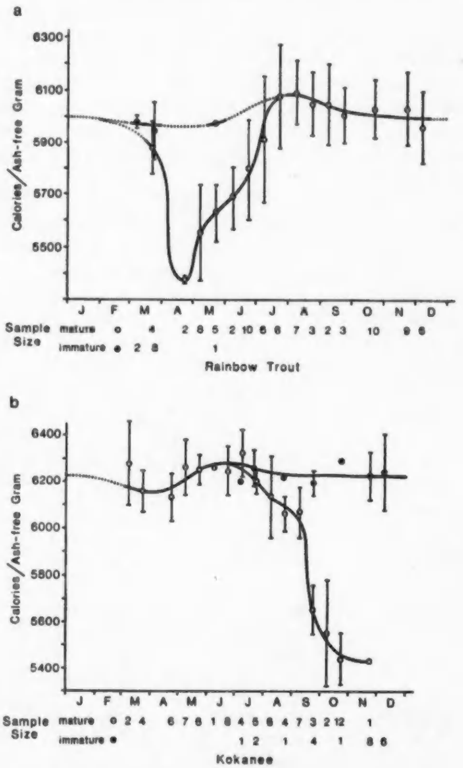


FIG. 7. Seasonal change in energy content (cal/ash-free g, mean ± standard deviation) of the fish excluding gonad. (a) rainbow trout (b) kokanee (Sandercock 1969).

that the growth rate of Marion Lake trout is among the lowest recorded. One reaches the same conclusion when comparing the growth of Marion Lake and other B.C. kokanee populations.

Biomass and production estimates are commonly used to make comparisons between fish populations in various systems. The biomass values for Marion Lake fish populations range from 8.9–28.9 kg/hectare (K. Hyatt unpublished data; Sandercock 1969). According to Carlander (1955) the normal range of biomass values in small "trout-lakes" is 9–32 kg/ha. This is almost identical to the range observed for Marion Lake fishes over the 10-yr duration of the project. The term production has a variety of definitions in fisheries management (Chapman 1967). In this section it is defined as the amount of energy (or biomass) elaborated in a specified period of time, whether or not all of it survives to the end of that time. Production is a function of both fish numbers and their growth rates. Annual production was 1.23×10^4 kcal/ha per year (9.8 kg/ha per year) for trout and 1.58×10^4 kcal/ha per year (11.7 kg/ha per year) for kokanee (Sandercock 1969). The range of production for salmonids in some lakes and reservoirs cited by Chapman (1967) is 19–156 kg/ha per year. Marion Lake with a total production of 21.5 kg/ha per year is at the low end of this range. Further, this is a maximum production estimate based on a total number of 13,000 fish, whereas calculations based on totals of 3500 fish would reduce this estimate by as much as 60% (K. Hyatt unpublished data).

RELATION OF FOOD TURNOVER TO FOOD SUPPLY

The initial research on fish populations in Marion Lake indicated that fish were generally slow growing. The mechanisms leading to low growth rate and resulting small body size and low production (especially as limited by food resources) were unclear. Consequently, the research was developed to emphasize factors determining food yield to the predator populations.

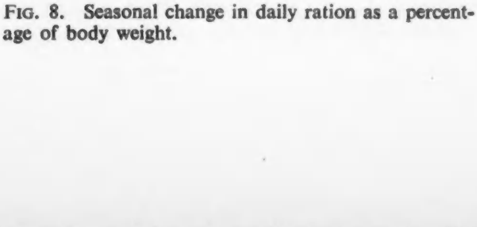


FIG. 8. Seasonal change in daily ration as a percentage of body weight.

Many techniques yield estimates of the total food consumed by fish populations. These range from estimates obtained from field experiments involving total removal of fish populations (Ball and Hayne 1952) to estimates that use various combinations of laboratory-determined and field-estimated data (Popova 1967; Ricker and Forester 1948; Allen 1951). Sandercock estimated the daily ration as percent of body weight for trout and kokanee in each month (Fig. 8) from the equation

$$\text{Daily ration} = \frac{\text{weight of food in digestive tract}}{\text{weight of fish}} \times$$
$$\text{food turnover rate} \times 100$$

If the yearly ration is calculated by extrapolating the estimated daily ration over a full year it appears that trout alone consume 1.6×10^8 kcal/hectare per year (approximately 112 kg/hectare per year). This estimate is probably inaccurate because it is based on few sampling dates, small sample sizes of fish, and crude estimates of food turnover time. The commonest technique to estimate food consumption of fish in the field is that of Winberg (treated in detail by Mann 1965, 1967), and is based on the assumption that energy content of the food equals the sum of the energy content of the material lost in egestion and excretion, the material retained in growth, and the material broken down in metabolism. By this technique, Sandercock determined that trout consume 10.72×10^4 kcal/hectare per year and kokanee 9.67×10^4 kcal/hectare per year. D. M. Ware (unpublished data) recalculated the food intake of the trout population, taking into account the relation between fish size, ration size, ambient temperature, and rate of digestion. His estimate was 4.6×10^4 kcal/hectare and suggests that those of Sandercock were too high. Using Ware's estimate of trout food intake and knowing the relative proportions of total food consumed by each of the vertebrate predators (Efford and Tsumura 1973) the estimate of food intake by the kokanee is 2.0×10^4 kcal/hectare per year.

It is useful for comparative purposes to have some measure of the efficiency with which fish crop their food supply. Gerking (1962) suggested that ideally we should relate the food turnover of a fish population to the total quantity and production rate of food organisms in the lake, the "available" food supply, and the "preferred" food supply.

Two convenient indices of the relationship of fish to their food are:

Trophic level production efficiency

$$= \frac{\text{Production at trophic level } t}{\text{Production at trophic level } t-1}$$

Ecotrophic coefficient (utilization efficiency)

$$= \frac{\text{Energy intake at trophic level } t}{\text{Energy production at trophic level } t-1}$$

For the Marion Lake fish population the estimated trophic level production efficiency ranges from 0.02 to 0.04, when production estimates are obtained by doubling the biomass values (I. E. Efford personal communication).

	Production (kcal/ha/yr)	Efficiency
Trout and kokanee, 1963 (Sandercock 1969)	2.8×10^4	
Benthic Invertebrates, 1969 (Hargrave 1969a)	76×10^4	.04
Benthic invertebrates, 1968–71 (I. E. Efford unpublished data)	158×10^4	.02

During the course of a year between 27 and 56 times more food than fish is produced. Gerking (1962) estimated that in Wyland Lake at least 10 times more food than fish is produced. Values calculated for the ecotrophic coefficient range from .04 to .23 (see table below). for fish in Marion Lake. The estimate for Wyland Lake bluegills was .48 and Gerking concluded that the efficiency of cropping the bottom fauna was high regardless of the standards used for comparison. Mann (1967) stated that from the various estimates of food intake of natural fish populations the same conclusion has emerged, namely that the food stocks are intensively grazed. By contrast the ecotrophic coefficient for the Marion Lake fish populations is the lowest on record, and regardless of the method chosen for comparison, they appear to be relatively *inefficient* at cropping the food supply.

Salmonid	Estimates of food intake (kcal/ha/yr)	Ecotrophic coefficient
Trout (Sandercock 1969)	9.1×10^4	.11–.23
Kokanee	8.2×10^4	
Total	17.3×10^4	
Trout Ware (1972)	4.6×10^4	.04–.09
Kokanee K. Hyatt (unpublished data)	2.0×10^4	
Total	6.6×10^4	

THE AVAILABLE FOOD SUPPLY

Nutrient procurement is never a random process. There are always identifiable mechanisms involved in the acquisition of specific nutrients over specific intervals of time, whether we are considering organization at the cellular level or at the whole organism level. For fish populations it is certainly an unwarranted assumption that there is a certain rate of production of food organisms that can be divided by the number of fish, to ascertain the ration eaten by each fish (Backiel and LeCren 1966). Larkin et al. (1956) suggested that in each lake a characteristic "availability" of food organisms determines the ratio of energy gained from food to energy expended in the living process. Therefore, if we are to explain the reasons for the particular level of production or food intake of a fish population, it is necessary to extend our already extensive qualitative knowledge of the diets of fish into an understanding of the mechanisms controlling the rates of consumption of the major prey organisms (LeCren 1965). Some of the controlling mechanisms are obvious but difficult to quantify; others are obscure because they may be due to properties more apparent to an ethologist or physiologist.

The sum of many complex interactions between predator, prey, and environment determines the availability of prey to predator. Much of the research on fish during the Marion Lake project has focused on describing and quantifying the importance of these interactions.

PROPERTIES OF THE ENVIRONMENT

Two properties of the environment are of particular importance to fish in Marion Lake. They are a temperature regime which varies seasonally and the complexity of the benthic substrates from which fish obtain most of their invertebrate prey.

The seasonal pattern of lake temperatures at 1 m and the energy intake of trout are presented in Fig. 9. The degree to which the patterns are similar is due to a parallel response of both maintenance requirement and feeding rate with temperature in fishes. However, energy intake during June–September is remarkably constant. This is not expected on the basis of the direct effect of temperature on feeding rate. This pattern is expected if: the fish are feeding at maximum capacity, the energy content of the prey has dropped, or the availability of prey has declined. The first two possibilities are not borne out by our data. However, the third explanation receives strong support. K. Hyatt (unpublished data) has described predictable seasonal shifts of both vertical and horizontal distribution of fishes in Marion Lake. Movements were related to high temperatures (>17 C) at the surface and in the littoral zone. If we consider the average distribution of one of the major prey species (*H. azteca*) and the distribution of trout (Fig. 10) under spring conditions (<15 C) and summer conditions (>17 C), it is clear that from July to September trout may be foraging in areas which have relatively low prey densities. Hyatt also found that significant numbers (approximately 15% of the population) of trout and kokanee remain in a large, central, cold spring when surface temperatures are greater than 20 C. As this part of the population was not taken into account when calculating the seasonal energy intake by fish, the actual intake is probably lower than that shown for July, August, and part of September.

Ware (1972) examined the effect of various substrates on the attack rate of trout on amphipods (*H. azteca* and *Crangonyx richmondensis*). He found that as the complexity of the mud and stick substrates increased the number of amphipods captured over time decreased. Further analysis revealed that trout did not respond to concealed animals and that the number of concealed animals increased as the substrate complexity increased. With the most complex substrate used the reduction in prey captured was approximately 85% as compared to the least complex. As the substrates Ware used were generally less complex than those found on the lake bottom this must be taken as a minimal estimate of their importance in providing refuge for some prey.

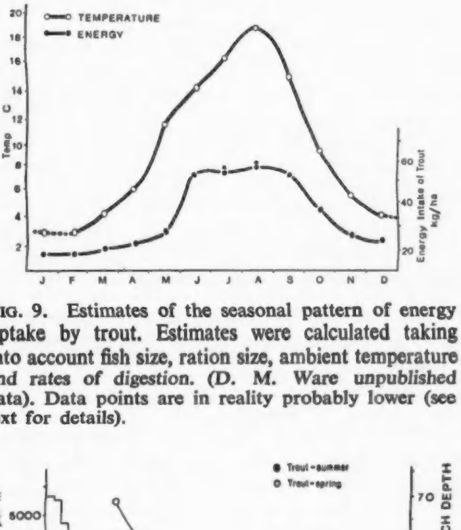


FIG. 9. Estimates of the seasonal pattern of energy uptake by trout. Estimates were calculated taking into account fish size, ration size, ambient temperature and rates of *digestion*. (*D. M. Ware unpublished* data). Data points are in reality probably lower (see text for details).

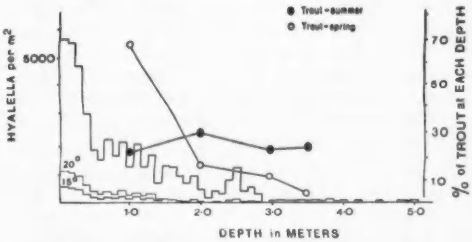


FIG. 10. Average density of *Hyalella azteca* in Marion Lake during the year as compared to the numbers exposed at two seasonal temperatures (15 and 20 C) and the density of trout at two times of year.

PROPERTIES OF THE PREDATORS

Each species of predator has a genotypic and phenotypic "makeup" which favors its success in some habitats rather than others. Tody (1964) summarized the results of several authors and reported that rainbow trout feed principally on benthic invertebrates. Foerster (1968) stated that the importance of zooplankton food cannot be too greatly stressed in regard to the production of sockeye salmon juveniles. Based upon this criterion Marion Lake should be much more suitable for rainbow trout production than for kokanee, as the production of benthic invertebrates is moderate and zooplankton production is very low (Efford 1969). It is difficult to determine the importance of genotype, but we may examine its phenotypic expression to identify the characteristics of the predators which limit food availability to them. Such characteristics may be morphological, physiological, or behavioral.

Keast and Webb (1966) have stressed the role that mouth and body form may play in the feeding ecology of freshwater fish. Shepherd (1970) measured mouth size in trout and kokanee ($n = 100$) and found that kokanee mouth width was much less than that of trout of the same size. Winterbourn (1971) found that trout in Marion Lake select the largest size-classes of caddis larvae available at all times of the year, whereas kokanee prey upon smaller species. Hyatt (Table 6) compared the percent capture success of kokanee and trout of approximately the same size and found that as prey size increased kokanee were much less successful at ingesting them than trout.

Trout and kokanee both depend on visual detection of prey at some point to complete a successful attack on a prey item (Ware 1973; K. Hyatt unpublished data). As many of the processes involved in distinguishing food from a background are shared by all visual feeders, Ware considered the mechanics of food location at a general level and coupled this with several additional features to evaluate trout searching for epibenthic prey. He found that size, contrast, and movement were all important prey characteristics which determined

TABLE 6. Relative capture success of trout and kokanee on different size-classes of prey (K. Hyatt unpublished data).

Prey type	Avg. size used (*mm*)	% capture success Kokanee (16 cm)	 Trout (15 cm)
Zooplankton *Daphnia* spp.	4	100	100
Amphipods *Hyalella* spp.	4	90	85
Crangonyx spp.	8	50	85
Damselfly *Enallagma* spp.	16	30	75

the distance at which trout would react to make an attack on an animal. Hyatt confirmed the importance of these characteristics in determining the reactive distance of kokanee to prey. The importance of these relations to prey availability becomes clear when considered in conjunction with particular aspects of predator behavior.

Ware (1973) pointed out that a predator will only attack a prey if the height of its searching position is less than the distance it requires to detect the prey visually. Ware indicated that in the laboratory trout maintain a fixed searching position. Hyatt described the seasonal and daily changes in searching position for both trout and kokanee in the field. Both species maintain a specific searching position when hunting for surface prey or benthic prey. This means that some size-classes of invertebrates will remain undetected and therefore unexploited by both kokanee and trout. *Hyallella* less than 3 mm are not captured by trout. Because kokanee maintain a position much closer to the benthic substrate ($\bar{x} = 2$ cm) than trout ($\bar{x} =$ 25 cm) they will be more effective predators of small inconspicuous organisms whereas trout would detect and exploit larger more conspicuous benthic organisms.

Properties of the Prey

The importance of size, contrast, and movement of prey has been suggested. Our analysis of other properties of prey organisms which determine prey availability to predators has revealed factors which affect seasonal changes in availability as well as those which affect instantaneous change of availability.

Ware (1973) found that changes in water temperature resulted both in changes to the average proportion of amphipods exposed above the mud-water interface and in amphipod activity per unit time. He concluded that even under the most favorable conditions in Marion Lake considerably less than 30% of the amphipods may be situated above the mud-water interface during daylight, whereas under the least favorable conditions as little as 2% of the population may be in a similar state of exposure. Recalling the effect of temperature on fish distribution, the importance of temperature in concert with predator and prey behavior is even more apparent. Figure 10 indicates the relative availability of *Hyalella* at two seasonal temperatures as compared to the actual density.

Borodic (1962; cited in Kajak and Dusoge 1971) stated that benthic invertebrates actively escape from fish by moving to deeper layers of sediments. Kajak and Dusoge examined the effects of bream on the vertical distribution of oligochaetes in sediments and found that when fish were present these invertebrates occurred in deeper layers of sediments than in the control aquarium without fish. Hyatt (Fig. 11) examined the effect of predator activity on the numbers of exposed mayfly larvae. It is clear that these prey respond dramatically to the presence of a predator, with the result that the instantaneous availability of prey to the predator diminished as a function of predator activity. This response is not specific just to fish, for it can be elicited by introducing any moving object to the tank. In the field this means that predators that forage in one small area will experience a decreasing probability of capture success, even though density of the prey remains relatively constant. Mechanisms such as this would act in a density-dependent fashion (i.e.

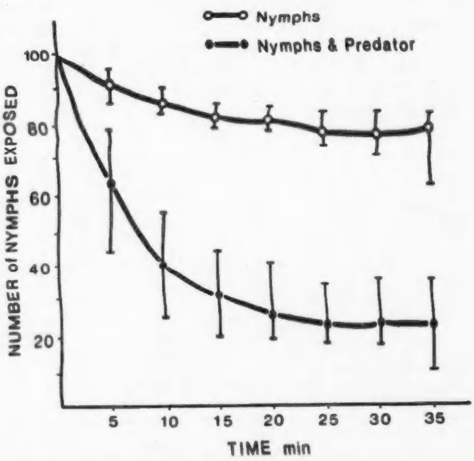


FIG. 11. The effect of predator activity on the numbers of exposed prey.

more predators — greater activity — fewer exposed prey). They also suggest that "depression competition" could take place between predators which have no food items in common but forage in the same area. However, such considerations are beyond the scope of the present paper.

MODELS

Results of experimental work described above indicate that the fish populations within the Marion Lake ecosystem are coupled in complex and intricate ways to their food resource. There has been a long history in ecology of grappling with such highly complex interactions between organisms and their environment. This has led to the production of various kinds of models with the aim of simplifying our understanding of the importance of various processes or components within the system. One of the most critical barriers to real progress in this endeavor was the inability to deal with more than a few interactions in a given model. With the development of applied computer techniques in ecology it became possible to deal with many more interactions, and since the 1960s there has been an intensive effort in modelling of ecosystems, of populations, and of ecological processes (see Walters 1971 and Holling 1972 for recent reviews).

Interest in synthesis of results from Marion Lake through mathematical models and simulation began in 1969 with a series of workshops among participants in the program. These workshops led to the development and testing of several types of models (Walters and Efford 1972), some of which were particularly relevant to predator–prey interactions between fish and benthic invertebrates.

Ware (1973) used an experimental components approach (Holling 1972) to develop a model describing the risk of aquatic prey to predation by rainbow trout. The model depended on several principles of visual mechanics to determine predation rates and required statistics on the physical properties of the food resource as well as estimates of the visual activity and other searching constraints on the predator (see Ware 1973 for details). Application of the model to an independent set of field data accounted for 47% of the seasonal variation in the occurrence of four benthic invertebrate prey in the diet of trout from Marion Lake. If only three of these prey were considered, the precision of the prediction increased to account for 70% of the seasonal variation. As the four prey comprised 69% by weight of the diet of trout, the model appears to represent a reasonable analogue of predation and the consequent yield of food to rainbow trout in Marion Lake.

The general applicability of Ware's model was restricted, as there was no allowance for altered prey risk under the influence of variables such as food palatability, food distribution, predator activity, variable success in capturing prey, etc. The problems of general applicability are particularly clear when comparing the dietary habits of trout as opposed to kokanee in Marion Lake. The four invertebrate prey in Ware's model which provided 69% of trout food intake, constitute only 18% by weight of the diet of kokanee. K. Hyatt (unpublished data) initiated a parallel study of the predatory behavior of kokanee in an attempt to expand the applicability of the model and found differences between the two species in habitat selection, foraging position, and success in capturing prey. Although we have not as yet introduced these modifications into the original model, they appear to be significant and hopefully will result in the production of a similar predictive model for kokanee predation.

Other models developed to deal with a large number of species and processes in the Marion Lake ecosystem have produced predictions relevant to the fish populations (see Efford and Walters 1973). Unrealistic predictions by such models have confirmed their utility in revealing the importance of key features that have been omitted as well as the importance of those that are taken into account. Recent attempts to explain or predict the results of predator–prey interactions in other fish populations (Kerr 1971a,b,c; Kerr and Martin 1970; Kitchell et al. 1972) have resulted in the production of predator–prey models similar to those developed for Marion Lake and indicate the increasing use and appreciation of models as tools by aquatic ecologists.

Conclusions

1, The numbers of fish in Marion Lake appear to vary widely over the period of a few years. Kokanee numbers are much more variable than those of trout.

2, Marion Lake fish production is low to moderate in comparison to other lakes producing salmonids.

3, Energy intake calculations indicate that trout and kokanee are relatively inefficient at cropping the benthic food supply.

4, There is a complex array of interactions between predators, prey, and their physical environment which determines the actual availability of prey to the predators.

5, The development of various simulation models during the course of the Marion Lake project has demonstrated their promise as a powerful tool in forwarding our understanding of complex interactions between organisms and their environment.

Acknowledgments

The authors wish to acknowledge Dr I. E. Efford for his support and encouragement in writing this review. We are greatly indebted to all the research scientists who participated in the Marion Lake IBP program from 1962–72 and made it a successful scientific endeavor. The diligence of S. Cosgrove and I. Yesaki in manuscript preparation and drafting is greatly appreciated.

Allen, K. R. 1951. The Horokiwi Stream: a study of a trout population. Fish. Bull. N.Z. 10: 1–238.

Bae, H. C., E. H. Cota-Robeles, and L. E. Casida, Jr. 1972. Microflora of soil as viewed by transmission electron microscopy. Appl. Microbiol. 23: 637–648.

Backiel, T., and E. D. LeCren. 1967. Some density relationships for fish population parameters, p. 315–344. *In* S. D. Gerking [ed.] The biological basis of freshwater fish production. Blackwell Scientific Publications, Oxford.

Ball, R. C., and D. W. Hayne. 1952. Effects of the removal of the fish population on the fish food-organisms of a lake. Ecology 33: 41–48.

Cameron, R. L. 1973. A comparison of the responses of benthic and planktonic communities to the enrichment of inorganic fertilizers. M.Sc. Thesis. Univ. British Columbia, Vancouver, B.C. 77 p.

Carlander, K. D. 1955. The standing crop of fish in lakes. J. Fish. Res. Board Can. 12: 543–570.

Chapman, D. W. 1967. Production in fish populations, p. 3–29. *In* S. D. Gerking [ed.] The biological basis of freshwater fish production. Blackwell Scientific Publications, Oxford.

Davies, G. S. 1970. Productivity of macrophytes in Marion Lake, British Columbia. J. Fish. Res. Board Can. 27: 71–81.

Dick, M. W. 1971. The ecology of Saprolegniaceae in lentic and littoral muds with a general theory of fungi in the lake ecosystem. J. Gen. Microbiol. 65: 325–337.

Dickman, M. 1969. Some effects of lake renewal on phytoplankton productivity and species composition. Limnol. Oceanogr. 14: 660–666.

Efford, I. E. 1967. Temporal and spatial differences in phytoplankton productivity in Marion Lake, British Columbia. J. Fish. Res. Board Can. 24: 2283–2307.

1969. Energy transfer in Marion Lake, British Columbia, with particular reference to fish feeding. Verh. Int. Ver. Limnol. 17: 104–108.

Efford, I. E., and K. Tsumura. 1973. A comparison of the food of salamanders and fish in Marion Lake, British Columbia. Trans. Am. Fish. Soc. 102: 33–47.

Foerster, R. E. 1968. The sockeye salmon. Bull. Fish. Res. Board Can. 162: 422 p.

Gaswami, K. P., and R. E. Green. 1971. A simple automatic soil percolator. Soil Biol. Biochem. 3: 389–391.

Gerking, S. D. 1962. Production and food utilization in a population of bluegill sunfish. Ecol. Monogr. 32: 31–78.

Gruendling, G. K. 1971. Ecology of the epipelic algal communities in Marion Lake, British Columbia. J. Phycol. 1: 239–249.

Hall, K. J., P. M. Kleiber, and I. Yesaki. 1972. Heterotrophic uptake of organic solutes by microorganisms in the sediment. Mem. Ist. Ital. Idrobiol. Suppl. 29: 441–471.

Hall, K. J., I. Yesaki, and S. Doel. 1973. Decomposition of leaf litter in sediment microcosms. 36th Meeting American Society of Limnol. and Oceanog., Univ. of Utah, Salt Lake City, Utah. June 10–14.

Hargrave, B. T. 1969a. Inter-relationships between a deposit-feeding amphipod and metabolism of sediment microflora. Ph.D. Thesis. Univ. British Columbia, Vancouver, B.C. 195 p.

1969b. Epibenthic algal production and community respiration in the sediments of Marion Lake. J. Fish. Res. Board Can. 26: 2003–2026.

1970. Distribution, growth, and seasonal abundance of *Hyalella azteca* (Amphipoda) in relation to sediment microflora. J. Fish. Res. Board Can. 27: 685–699.

Holm-Hansen, O., and C. R. Booth. 1966. The measurement of adenosine triphosphate in the ocean and its ecological significance. Limnol. Oceanogr. 11: 510–519.

Holling, C. S. 1972. Ecological models: a status report. Proc. International Symp. Math. Model. Tech. Water Res. Syst. 1: 3–20.

Johnson, W. E. 1965. On mechanisms of self-regulation of population abundance in *Oncorhynchus nerka*. Mitt. Int. Ver. Angew. Limnol. 13: 66–87.

Kajak, Z., and K. Dusoge. 1971. The regularities of vertical distribution of benthos in bottom sediments of three Masurian lakes. Ekol. Pol. 29: 485–499.

Kaushik, N. K., and H. B. N. Hynes. 1971. The fate of the dead leaves that fall into streams. Arch. Hydrobiol. 68: 465–515.

Keast, A., and D. Webb. 1966. Mouth and body form relative to feeding ecology in the fish fauna of a small lake, Lake Opinicon, Ontario. J. Fish. Res. Board Can. 23: 1845–1874.

Kerr, S. R. 1971a. Analysis of laboratory experiments on growth efficiency of fishes. J. Fish. Res. Board Can. 28: 801–808.

1971b. Prediction of fish growth efficiency in nature. J. Fish. Res. Board Can. 28: 809–814.

1971c. A simulation model of lake trout growth. J. Fish. Res. Board Can. 28: 815–819.

Kerr, S. R., and N. V. Martin. 1970. Trophic-dynamics of lake trout production systems, p. 365–376. *In* J. H. Steele [ed.] Marine food chains. Univ. California Press, Berkeley, Calif.

Kitchell, J. F., J. F. Koonce, R. V. O'Neill, J. J. Magnuson, and R. S. Booth. 1972. Implementation of a predator-prey biomass model for fish.

Memo report #72–118, Univ. Wisconsin, Madison, Wis. 56 p.

Kleiber, P. M. 1972. The dynamics of extracellular, dissolved organic material in the sediments of Marion Lake, British Columbia. Ph.D. Thesis. Univ. California, Davis, Calif. 93 p.

Larkin, P. A., J. G. Terpenning, and R. R. Parkes. 1956. Size as a determinant of growth rate in rainbow trout. Trans. Am. Fish. Soc. 86: 84–96.

LeCren, E. D. 1958. Observations on the growth of perch (*Perca fluviatilis*) over twenty-two years with special reference to the effects of temperature and changes in population density. J. Anim. Ecol. 27: 287–334.

1965. Some factors regulating the size of populations of freshwater fish. Mitt. Int. Verein. Limnol. 13: 88–105.

Lee, C. C., R. F. Harris, J. D. H. Williams, D. E. Armstrong, and J. K. Seyers. 1971. Adenosine triphosphate in lake sediments. Soil Sci. Soc. Am. Proc. 35: 82–91.

Mann, K. H. 1965. Energy transformations by a population of fish in the River Thames. J. Anim. Ecol. 34: 253–275.

1967. The cropping of the food supply, p. 243–257. *In* S. D. Gerking [ed.] The biological basis of freshwater fish production. Blackwell Scientific Publications, Oxford.

Mathewes, R. 1973. Paleoecology of postglacial sediments in the Fraser lowland region of British Columbia. Ph.D. Thesis. Univ. British Columbia, Vancouver, B.C. 77 p.

Melchiorri-Santolini, U., and J. W. Hopton [ed.]. 1972. Detritus and its role in aquatic ecosystems. Proc. IBP-UNESCO Symp. Pallanza, Italy. 540 p.

Odum, E. P., and A. A. de la Cruz. 1963. Detritus as a major component of ecosystems. Am. Inst. Biol. Sci. Bull. 13: 39–40.

Popova, O. A. 1967. The 'predator-prey' relationship among fish, p. 359–376. *In* S. D. Gerking [ed.] The biological basis of freshwater fish production. Blackwell Scientific Publications, Oxford.

Ramey, W. D. 1972. Microscopic examination of bacterial population within the detritus of Marion Lake. Univ. British Columbia, Vancouver, B.C. 28 p. (undergraduate paper)

Ricker, W. E., and R. E. Forester. 1948. Computation of fish production. Bull. Bingham Oceanogr. Collect. Yale Univ. 11: 193–211.

Rodina, A. G. 1972. Methods in aquatic microbiology. Univ. Park Press, Baltimore, Md. 461 p.

Sandercock, F. K. 1969. Bioenergetics of the rainbow trout (*Salmo gairdneri*) and the kokanee (*Oncorhynchus nerka*) populations of Marion Lake, British Columbia. Ph.D. Thesis. Univ. British Columbia, Vancouver, B.C. 165 p.

Shepherd, B. 1970. Aspects of the feeding behaviour of the rainbow trout (*Salmo gairdneri*) and kokanee (*Oncorhynchus nerka*) of Marion Lake, British Columbia. Univ. British Columbia, Vancouver, B.C. 52 p. (undergraduate paper)

Sorokin, Y. I., and H. Kadota [ed.] 1972. Techniques for the assessment of microbial production and decomposition in fresh water. I.B.P. Handbook No. 23. Blackwell Scientific Publications, Oxford. 112 p.

Tody, W. H. 1964. An investigation of the success of rainbow trout populations in ten lakes relative to limiting environmental factors. Ph.D. Thesis. Michigan State Univ., East Lansing, Mich. 166 p.

Walters, C. J. 1971. Systems ecology: the systems approach and mathematical models in ecology, p. 267–292. *In* E. P. Odum [ed.] Fundamentals of ecology. 3rd ed. W. B. Saunders Co.

Walters, C. J., and I. E. Efford. 1972. Systems analysis in the Marion Lake I.B.P. project. Oecologia (Berl.) 11: 33–44.

Ware, D. M. 1972. Predation of rainbow trout (*Salmo gairdneri*): the influence of hunger, prey density and prey size. J. Fish. Res. Board Can. 29: 1193–1201.

1973. Risk of epibenthic prey to predation by rainbow trout (*Salmo gairdneri*). J. Fish. Res. Board Can. 30: 787–797.

Winterbourn, M. J. 1971. An ecological study of *Banksiola crotchi* Banks (Trichoptera, Phryganeidae) in Marion Lake, British Columbia. Can. J. Zool. 49: 637–645.

PUBLICATIONS

Additional papers dealing with some aspect of the ecology or biology of Marion Lake accepted for publication up to Jan. 1, 1974.

Conroy, J. S. 1968. The water-mites of Western Canada. Natl. Mus. Can. Bull. 223: 23–42.

1973. A new method for trapping water-mites in the benthos of a lake. Proc. III. Int. Congr. Acarol., Prague, 1971: 151–157. (In press)

Calef, G. W. 1973. Natural mortality of tadpoles in a population of *Rana aurora*. Ecology 54: 741–758.

1973. Spatial distribution and "effective" breeding population of red-legged frogs in Marion Lake, British Columbia. Can. Field Nat. 87: 279–284.

Davies, R. W., and V. J. McCauley. 1970. Effects of preservatives on the regurgitation of the gut contents of Chironomidae (Diptera) larvae. Can. J. Zool. 48: 519–522.

Dick, M. W. 1970. Saprolegniaceae on insect exuviae. Trans. Br. Mycol. Soc. 55: 449–458.

Dickman, M. D. 1968. A new method for making permanent phytoplankton mounts. Hyrdobiologia 31: 161–167.

1968. Some indices of diversity. Ecology 49: 1191–1193.

1968. The effect of grazing by tadpoles on the structure of a periphyton community. Ecology 49: 1188–1190.

1974. Changes in phytoplankton following nitrate and phosphate additions to large enclosures in Marion Lake, British Columbia. Schweiz. Z. Hydrol. (In press)

Dickman, M. D., and I. E. Efford. 1972. Some effects of artificial fertilization on enclosed plankton populations in Marion Lake, British Columbia. J. Fish. Res. Board Can. 29: 1595–1604.

Efford, I. E. 1972. An interim review of the Marion Lake project, p. 89–109. *In* Z. Kajak and A. Hillbricht-Ilkowska [ed.] Productivity problems of freshwaters, Warsaw. Proc. UNESCO-IBP Synp. Prod. Problems Freshwaters. Kazimierz Dolny, Poland.

1974. Ecosystem components–An essay on the structure of aquatic systems. Can. Bot. Assoc. (In press)

Efford, I. E., and J. A. Mathias. 1969. A comparison of two salamander populations in Marion Lake, British Columbia. Copeia 4: 723–736.

Efford, I. E., and K. Tsumura. 1969. Observations on the biology of the Trematode *Megalodiscus microphagus* in amphibians from Marion Lake, British Columbia. Am. Midl. Nat. 82: 197–203.

1974. Uptake of dissolved glucose and glycine by *Pisidium*, a freshwater bivalve. Can. J. Zool. (In press)

Hargrave, B. T. 1969. Similarity of oxygen uptake by benthic communities. Limnol. Oceanogr. 14: 801–805.

1970a. The utilization of benthic microflora by *Hyalella azteca* (Amphipoda). J. Anim. Ecol. 39: 427–437.

1970b. The effect of a deposit-feeding amphipod on the metabolism of benthic microflora. Limnol. Oceanogr. 15: 21–30.

1971. An energy budget for a deposit-feeding amphipod. Limnol. Oceanogr. 16: 99–103.

1972. Prediction of egestion by the deposit-feeding amphipod *Hyalella azteca*. Oikos 23: 116–124.

Henderson, B. A. 1973. The specialized feeding behaviour of *Ambystoma gracile* in Marion Lake, British Columbia. Can. Field Nat. 87: 151–154.

Licht, L. W. 1969. Comparative breeding behaviour of the red-legged frog (*Rana aurora aurora*) and the western spotted frog (*Rana pretiosa pretiosa*) in Southwestern British Columbia. Can. J. Zool. 47: 1287–1299.

Lindsey, C. C. 1966. Temperature-controlled meristic variation in the salamander *Ambystoma gracile*. Nature 209: 1152–1153.

Mathewes, R. 1974. A palynological study of postglacial vegetation changes in the University Research Forest, southwestern British Columbia. Can. J. Bot. (In press)

Mathias, J. A. 1971. Energy flow and secondary production of the amphipods *Hyalella azteca* and *Crangonyx richmondensis occidentalis* in Marion Lake. J. Fish. Res. Board Can. 28: 711–726.

McQueen, D. J. 1969. Reduction of zooplankton standing stocks by predaceous *Cyclops bicuspidatus thomasi* in Marion Lake, British Columbia. J. Fish. Res. Board Can. 26: 1605–1618.

1970. Grazing rates and food selection in *Diaptomus oregonensis* (Copepoda) from Marion Lake, British Columbia. J. Fish. Res. Board Can. 27: 13–20.

Neish, I. C. 1971. Comparison of size, structure and distributional patterns of two salamander populations in Marion Lake, British Columbia. J. Fish. Res. Board Can. 28: 49–58.

Pearlstone, P. 1973. Food of damselfly larvae in Marion Lake, British Columbia. Syesis. 6: 33–39.

Procter, D. 1973. The effect of temperature and photoperiod on larval development in Odonata. Can. J. Zool. 51: 1165–1170.

Sæther, O. A. 1969. Some Nearctic Podonominae, Diamesinae and Orthocladiinae (Diptera: Chironomidae). Fish. Res. Board Can. Bull. 170: 154 p.

1973. Taxonomy and ecology of three new species of *Norodiamesa* Kieffer, with keys to Nearctic and Palearctic species of the genus (Diptera: Chironomidae). J. Fish. Res. Board Can. 30: 665–679.

Scudder, G. G. E. 1971. The Gerridae (Hemiptera) of British Columbia. J. Entomol. Soc. B.C. 68: 3–10.

Shepherd, B. G. 1973. Transmitter attachment and fish behaviour. Underwater Telem. Newsl. 3: 8–11.

Stein, J. R., and J. F. Gerrath. 1968. Freshwater algae of British Columbia: desmids of bog lakes in coast mountain area. Syesis 1: 187–197.

Wali, M. K., G. K. Gruendling, and D. W. Blinn. 1972. Observations on the nutrient composition of a freshwater lake ecosystem. Arch. Hydrobiol. 69: 452–464.

Wallen, D. G., and G. H. Geen. 1968. Loss of radioactivity during storage of ^{14}C labelled phytoplankton on membrane filters. J. Fish. Res. Board Can. 25: 2219–2224.

Weiser, J., and V. J. McCauley. 1971. Two *Coelomomyces* infections of Chironomidae (Diptera) larvae in Marion Lake, British Columbia. Can. J. Zool. 49: 65–68.

1972. Validation of a new species and a new variety of *Coelomomyces* (Blastocladiales: Coelomomycetaceae) described from Marion Lake, British Columbia. Can. J. Zool. 50: 365.

Winterbourn, M. J. 1971. The life histories and trophic relationships of the Trichoptera of Marion Lake, British Columbia. Can. J. Zool. 49: 623–635.

THESES COMPLETED

Obtainable through the library, University of British Columbia, Vancouver 8, B.C.

Ph.D.

Calef, G. 1971. An analysis of mortality in a population of tadpoles of the red-legged frog (*Rana aurora*). 67 p.

Conroy, J. 1973. Ecology of watermites in Marion Lake. (University of Manitoba) 155 p.

Dickman, M. D. 1968. The relation of freshwater plankton productivity to species composition during induced successions. 115 p.

Hamilton, A. L. 1965. An analysis of a freshwater benthic community with special reference to the Chironomidae. 94 p.

Jamieson, G. 1973. Coexistence in the gerridae. 225 p.

Neish, I. C. 1970. A comparative analysis of the feeding behaviour of two salamander populations in Marion Lake, British Columbia. 108 p.

Ware, D. M. 1971. The predatory behaviour of rainbow trout (*Salmo gairdneri*). 158 p.

M.Sc.

Bryan, A. D. 1971. Some aspects of the behavioural ecology of two amphipod species in Marion Lake, British Columbia. 61 p.

Davies, G. S. 1968. The productivity of macrophytes of Marion Lake, British Columbia. 28 p.

Gerrath, J. F. 1965. Desmids of some lakes in southwestern British Columbia with observations on *Triploceras* in culture. 73 p.

Mathias, J. A. 1967. Population energetics of two amphipod species in Marion Lake. 74 p.

Maynard, K. J. 1969. A population study of waterstriders (Gerridae: Hamiptera) in Marion Lake, British Columbia. 43 p.

McQueen, D. J. 1967. Studies of feeding activities of copepods in Marion Lake, British Columbia. 53 p.

Pearlstone, P. S. M. 1971. Observations of a natural population of damselfly larvae. 54 p.

Procter, D. 1971. The effects of temperature and photoperiod on the duration of larval development in three species of Odonata. 26 p.

Shepherd, B. G. 1973. Temporal and spatial differences in movement of cutthroat trout in Placid Lake, British Columbia. 92 p.

Starr, P. 1973. Colonization of lilypads by *Sida crystallina* in Marion Lake, British Columbia. 74 p.

Whitney, C. 1973. A study of territorial and vocal behaviour of the tree frog (*Hyla regilla*). 90 p.

B.Sc.

Davies, G. S. 1964. Some aspects of the biology of the plankton of Marion Lake. 37 p.

DeLury, R. T. 1971. Host-parasite system of *Menetus cooperi* (Gastropoda: Planorbidae) and *Megalodiscus microphagus* (Trematoda: Paramphistomatidae) in Marion Lake, British Columbia. 50 p.

Fairbairn, B. 1970. Energy distribution in the salamander *Ambystoma gracile*. 83 p.

Healey, F. P. 1964. Phytoplankton productivity and chlorophyll studies on a small lake. 37 p.

Henderson, B. A. 1970. Some biology and the feeding behaviour of *Ambystoma gracile* in Marion Lake, British Columbia. 37 p.

Lee, E. 1967. Some aspects of the energy budget of the family Planorbidae in Marion Lake. 53 p.

Mathias, J. A. 1964. Some aspects of the biology of *Taricha granulosa*. 37 p.

Theses in Progress

Ph.D.

Chang, C-Y. Fungi imperfecti in Marion Lake sediments.

Hoebel, M. Ecology of benthic rotifers.

Hyatt, K. A comparison of the ecology of rainbow trout and kokanee in Marion Lake.

M.Sc.

Kool, R. The ecology of the ciliated Protozoa in Marion Lake, British Columbia.

Perry, E. The biomass and activity of benthic bacteria in Marion Lake, British Columbia.

Effects of Hydroelectric Development in Western Canada on Aquatic Ecosystems[1]

GLEN H. GEEN

Department of Biological Sciences
Simon Fraser University, Burnaby, B.C.

GEEN, G. H. 1974. Effects of hydroelectric development in western Canada on aquatic ecosystems. J. Fish. Res. Board Can. 31: 913–927.

The effects of some existing and proposed hydroelectric developments on lakes and rivers of Western Canada are considered. There are few pre- and postimpoundment studies from this region on which to base generalizations, although the changes in species composition and water chemistry following impoundment of rivers and lakes reported thus far are comparable to those observed in other areas at similar latitudes. Few data are available which permit prediction of thermal regimes in newly formed reservoirs, particularly in view of the turbid nature of some inflows to reservoirs. Several hydroelectric developments have blocked or impeded migrations of economically important fish and appear likely to produce a number of downstream changes in water temperature or composition, the effects of which are often speculative. More studies of the effects of altered temperature and flow regimes, reduced turbidity, and gas supersaturation are required.

GEEN, G. H. 1974. Effects of hydroelectric development in western Canada on aquatic ecosystems. J. Fish. Res. Board Can. 31: 913–927.

Nous examinons les effets de certains développements hydroélectriques actuels ou en perspective sur les lacs et les rivières de l'Ouest canadien. Il existe peu d'études d'avant et d'après retenue pour cette région qui permettent de faire des généralisations. Cependant, les changements de composition spécifique et de chimie de l'eau à la suite de l'établissement d'un réservoir de retenue dans des rivières et des lacs ont été, à venir jusqu'ici, comparables à ceux observés dans d'autres régions situées aux mêmes latitudes. Il y a peu de données de disponibles permettant de prédire les régimes thermiques dans des réservoirs nouvellement formés, particulièrement en regard de la turbidité de certaines entrées d'eau dans ces réservoirs. Plusieurs développements hydroélectriques ont bloqué ou entravé les migrations de poissons d'importance économique et, vraisemblablement, produiront plusieurs changements de température ou de composition de l'eau en aval, changements dont les effets sont souvent conjecturaux. On a besoin d'étudier davantage les effets de changements de régimes de température et de débit, d'une turbidité réduite et d'une supersaturation des gaz.

Accepted January 17, 1974

THE demand for additional electric power in Western Canada is at present most frequently satisfied by hydroelectric power generation. These developments, which are often the subject of considerable controversy in the public sector, generally produce major changes in the lakes or rivers which are dammed to provide the necessary water storage. This paper reviews some changes in the aquatic environments resulting from hydroelectric development. Discussion is restricted to a detailed examination of the few developments in western Canada whose effects have been well documented through pre- and postimpoundment studies. The numerous reports assessing possible effects of a proposed development are generally not considered, as they contribute little to the formulation of generalizations unless followed by postdevelopment study. Probable consequences of several of the large hydroelectric developments which are being planned or are under construction are included because a major environmental impact is anticipated.

Additional information and other perspectives on the sociological, economic, and biological consequences of hydroelectric developments are in Larkin (1958) and Efford and Smith (1972).

This paper is organized on a regional basis for convenience and considers developments from Manitoba west through British Columbia and

---

[1] This paper, part of a special issue that comprises a comprehensive review of Limnology in Canada, was prepared to mark the 19th Congress of the International Association of Limnology (SIL), in Winnipeg, Man., during August 1974.

Printed in Canada (J3283)

north to the Northwest Territories and the Yukon. The extent of coverage may appear uneven; this reflects regional differences in the number of hydroelectric developments. Most attention is centered on Alberta and British Columbia.

The general geological, climatic, and limnological features of western Canada are described by Northcote and Larkin (1963). The area is divisible into two major physiographic regions — the western plains and subarctic which drain to the arctic, and the mountainous cordillera on the western slope of the continental divide. The cordilleran region is mainly the Province of British Columbia, whereas Alberta, Saskatchewan, and Manitoba spread across the northern great central plains and extend north into the Canadian Shield. With the exception of coastal British Columbia, the climate is continental with warm summers, cold winters, and low precipitation. Peak runoff usually occurs sometime between April and August. This seasonal peak in discharge is often stored for subsequent generation of hydroelectric power.

There are also differences in the complex of fish species in these two areas. On the west coast the anadromous Pacific salmon (*Oncorhynchus* spp.) and rainbow trout (*Salmo gairdneri*) are frequently of principal concern when new hydroelectric plants are developed. In the plains and arctic areas, fishery problems usually center on lake whitefish (*Coregonus clupeaformis*), lake trout (*Salvelinus namaycush*), walleye (*Stizostedion vitreum vitreum*), ciscoes (*Coregonus* spp.), Arctic grayling (*Thymallus arcticus*), or northern pike (*Esox lucius*). Regional differences in zooplankton and bottom fauna composition also occur. Most of the attention concerning effects of proposed hydroelectric developments has been focused on fish populations.

British Columbia

The most extensive hydroelectric development in western Canada has occurred in British Columbia. Domestic requirements of the relatively large and rapidly growing population coupled with major industrial needs have created a demand for electric power which has largely been met by hydroelectric developments in the following areas: coastal streams of mainland B.C. and Vancouver Island, streams tributary to the Fraser River, the Peace River, and the Columbia and Kootenay rivers. Sites of major developments in these areas are indicated in Fig. 1.

There have been several hydroelectric developments on the B.C. coast and Vancouver Island. None are particularly large, but most have led to a resource-use conflict between developers and agencies responsible for management and protection of salmon and trout populations. Efforts have been made to minimize the effects of these projects, several of which are described briefly by Larkin et al. (1959), by installation of fishways, provision of a guaranteed minimum downstream flow, or construction of artificial spawning channels.

Fishways often provide adequate access for salmon or trout over low-head installations. In many areas where a development is likely to produce major losses to salmonids, artificial spawning channels are being used with increasing frequency and success to ensure maintenance of the affected fish populations. These channels are usually excavated adjacent to the original stream bed. Gravel of optimum size for spawning fish is placed on the channel bottom and a regulated flow passed down the channel. Survival of eggs and alevins in these channels is frequently substantially above that

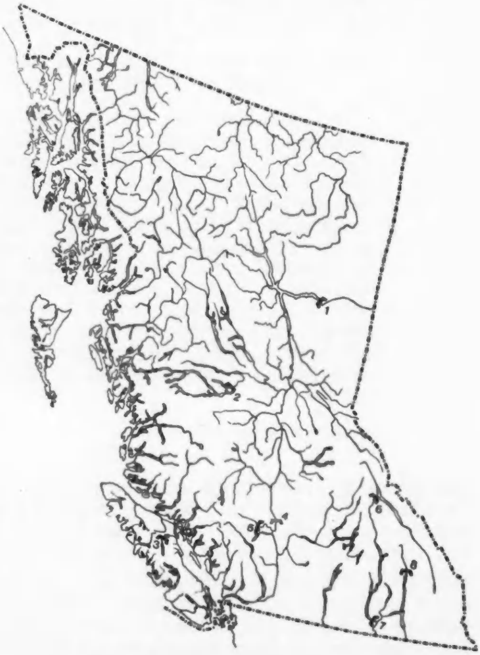


FIG. 1. Location of the hydroelectric developments in British Columbia whose effects are considered in this paper: 1. W.A.C. Bennett Dam on the Peace River; 2. Kenney Dam on the Nechako River; 3. Approximate location of Ladore Dam on Lower Campbell Lake and Strathcona Dam on Upper Campbell Lake; 4. Proposed site of the Moran Dam; 5. Trezaghi Dam on Bridge River which diverts water to Seton Lake; 6. Mica Dam on the Columbia River; 7. Hugh Keenleyside Dam on the Arrow Lakes; 8. Duncan Dam on the outlet of Duncan Lake.

observed in nature. These channels have proved so successful that they are also being used to increase salmon populations in areas unaffected by hydroelectric development (MacKinnon et al. 1961; Lucas 1960; Mead and Woodall 1968; MacKinnon 1960).

In British Columbia the only detailed pre- and postimpoundment studies have been conducted on the Campbell River system, especially on Buttle and Lower Campbell lakes, which flow into the upper part of the Gulf of Georgia via the Campbell River (Fig. 1). Ladore Dam was constructed at the outlet of Lower Campbell Lake in 1949. In 1958 Upper Campbell and Buttle lakes were flooded by construction of Strathcona Dam at the outlet of Upper Campbell Lake. Elevations of Buttle Lake and Lower Campbell Lake were increased by 9 and 17 m, respectively. Details of pre- and postimpoundment conditions were reported by Carl (1937), McMynn and Larkin (1953), and Sinclair (1965).

Sinclair (1965) considered the effects of water level fluctuations on the limnology of these two lakes. Seasonal changes in water level are now 3.5 m in Lower Campbell Lake and 5.5 m in Buttle Lake. Sinclair noted that no major postimpoundment physical or chemical changes in the water were evident in either lake. There was no difference in settled volumes of plankton after the development, although the cladoceran *Holopedium* sp. was abundant following regulation but not recorded during preimpoundment studies.

Reservoir clearing was required before these lakes were flooded. The forest surrounding Buttle Lake was primarily mature conifers. Trees were cut close to the ground and all waste material was burned. Most of the area surrounding Lower Campbell Lake was densely covered with young second growth conifers. The few remaining large trees were removed but the second growth was left to break down and decay underwater.

In Buttle Lake the cleared zone subject to fluctuating water levels became little more than a large sterile gravel bar as a result of wave action and erosion. Silt accumulated in the littoral area immediately below the drawdown limit and in the preimpoundment littoral area. However, in Lower Campbell Lake erosion was much less serious because the zone of regulation had not been denuded of its vegetation in the same way. Some sediments were transported to the preimpoundment littoral area, but not as much as in Buttle Lake.

Major changes were evident in bottom samples from both lakes. In Buttle Lake all organisms were much less abundant following impoundment; amphipods (*Hyalella knickerbockeri*) and stonefly nymphs were completely absent. Amphipods were completely absent from Lower Campbell Lake, although total abundance was low before impoundment. The absence of amphipods was associated with the postimpoundment disappearance of rooted aquatic plants. Oligochaetes, chironomids, and pisidians in both lakes were distributed in an inverted bathymetric manner with greatest numbers occurring in the littoral immediately below the drawdown limit. Chironomids decreased in both lakes following impoundment, contrary to trends observed in other areas (see for example, Nursall 1952).

This study is one of the few of its kind in Canada. It provides some important guidance on reservoir clearing practices. Evidently, complete removal of all terrestrial vegetation around the shoreline prior to flooding can lead to considerable erosion in exposed areas and silting in deeper areas of the lake. If clearing is confined to removal of larger trees, the smaller remaining vegetation may provide a measure of soil stability, minimize erosion, and provide a more favorable environment for development of benthic invertebrate populations.

The Fraser River system, the most important salmon producer in British Columbia, has thus far been developed for hydroelectric power generation to a relatively minor extent, but is the focus of frequent proposals for generation of large quantities of hydroelectric power. The economic significance of the salmon produced in this river system has meant that salmon management agencies have viewed such proposals with justifiable concern. Thus far, a relatively small number of tributaries have been developed. Effects of two of the existing developments on Fraser River tributaries will be reviewed briefly. Detailed consideration will also be given to one of the major proposals for main stem development of the Fraser River.

Since 1934, water has been diverted for power generation from Bridge River to Seton Lake, some 400 m lower in elevation (Fig. 1). At first the diverted flow was small, but it increased to 84 m^3/s by 1960. This resulted in a major reduction in flow in the Bridge River downstream of the diversion dam, a probable reduction in Bridge River chinook salmon (*O. tshawytscha*) populations, and diversion of a substantial volume of turbid water to the previously clear, oligotrophic Seton Lake.

Geen and Andrew (1961) examined the effects of this diversion on Seton Lake by comparing conditions with those in Anderson Lake, a large oligotrophic lake 3 km upstream, which by virtue of comparable morphometry, probably represented conditions in Seton Lake prior to the diversion. They suggested that the apparent decrease in temperature and TDS and the increase in turbidity and flushing rate were responsible for a dramatic reduction in zooplankton standing crop. Growth of young sockeye salmon in Seton Lake did not decrease as might have been expected, given the presumed reduction of standing crop of zooplankton. However, the numbers of young sockeye in this system at that time were sufficiently low that the reduction in food supply was probably of little consequence.

Diversion of cold water to Seton Lake may have benefited pink salmon spawning in Seton Creek, the outlet of Seton Lake. Prior to diversion there was an indication that temperatures during the fall spawning period were occasionally sufficiently high to have an adverse effect on spawning and egg survival. The reduction of stream temperature resulting from diversion has probably improved spawning and incubation conditions for pink salmon (Geen and Andrew 1961).

Downstream effects following diversion have also been of concern on the Nechako River. Most of the water from the Ootsa–Whitesail–Tahtsa chain of lakes, which originally flowed to the Fraser River via the Nechako River, has been diverted to a generating station at Kemano near the coast of B.C. by construction of a dam on the Nechako River (Fig. 1). This resulted in a reduced flow in the Nechako River, a migratory route for sockeye destined for the Stellako, Stuart, and Nadina river systems. Temperatures in this reduced flow are occasionally above the limits generally accepted as lethal to adult salmon, and concern has been expressed that spawning might be reduced. This concern could be alleviated by drawing at least a portion of the guaranteed minimum downstream flow from below the thermocline of the reservoir rather than solely from the surface. Thus far there have been no concerted efforts to assess the effects of the increase in summer temperatures, although no significant increase in mortality of unspawned salmon has been reported.

One of the most controversial suggestions for hydroelectric development in B.C. is the proposal for construction of a high-head dam at Moran Canyon on the Fraser River approximately 360 km upstream from its mouth (Fig. 1). Studies evaluating consequences to Pacific salmon of such proposals have been underway for more than 20 yr, and are reviewed in some detail here to indicate the effects a high-head development could have on salmon stocks of any major river. Extensive reviews of the effects of a Moran-type dam on Pacific salmon have previously been prepared (Brett 1957; Andrew and Geen 1960; Anon. 1971a; Geen 1972).

Exact details of the various proposals for a dam at Moran Canyon have varied, but all have involved a dam over 210 m high which would create a reservoir extending approximately 270 km upstream to the vicinity of Quesnel. The annual range in reservoir elevation could exceed 50 m.

Five species of Pacific salmon occur in the Fraser River system. Two of these, sockeye (*O. nerka*) and chinook (*O. tshawytscha*), occur in substantial numbers upstream of Moran Canyon. The sockeye stocks, which are increasing in size, are the most important and may number more than a million upstream migrant adults past Moran Canyon per year. Facilities have yet to be designed that would be able to handle quickly the number of adult salmon requiring passage over a high-head dam. That a delay is associated with collection and passage of adult salmon at dams is well known. It is equally well documented that adult Fraser River sockeye salmon are able to tolerate only limited delay as their energy reserves are closely tied to the requirements necessary for successful migration and spawning (Idler and Clemens 1959). Any delay at Moran Dam would likely be of sufficient length to significantly reduce energy reserves and seriously reduce spawning success.

Downstream migration of juvenile salmon through the reservoir and over the dam would also result in major losses. No effective methods for collecting large numbers of young salmon from reservoirs or the forebay of a large dam have been developed. Thus, migrants in the reservoir may go over the spillway or through the turbines and suffer considerable mortality or become residual in the reservoir and, in the case of sockeye, develop into the small landlocked form known as the kokanee.

The creation of a 270 km long reservoir behind Moran Dam would have significant downstream effects. Water for the turbines would be taken from considerable depths and probably from below the summer thermocline. It has been predicted (Andrew and Geen 1960; Anon. 1971a) that downstream water temperatures would be lower than present in summer and higher in fall. The elevated fall temperature would be expected to increase the rate of development of those salmon, primarily pinks, spawning in the lower part of the river. This would result in earlier emergence and seaward migration. Consequently, young pinks might arrive in the Gulf of Georgia at a time which did not coincide with favorable feeding conditions in the marine environment, and marine mortality would likely increase.

Parsons (1972) has considered effects of the changes in flow, temperature, and turbidity resulting from a Moran-type dam on productivity in the Gulf of Georgia, the coastal area into which the Fraser River flows. Early spring productivity in the Fraser River plume is high and is related to the early onset of water column stability and an entrainment of nutrient-rich deep water as the Fraser River water moves out over the more saline Gulf water. The anticipated increase in winter flows of the Fraser River following regulation would increase the areal extent of this productive plume, which could increase total phytoplankton and zooplankton production. However, Fraser River temperatures during April and May would likely be somewhat lower than at present (Andrew and Geen 1960; Anon. 1971a). This could retard development of the copepods on which young salmon feed. A larger standing crop of phytoplankton might therefore develop given the expected turbidity reduction of Fraser River water and in the absence of as intense copepod grazing. This increased phytoplankton standing crop in the plume might be more available to benthic organisms. The slower copepod development associated with this temperature reduction could also adversely affect survival of young salmon, which are dependent for food on the later developmental stages of copepods such as *Calanus plumchrus*.

Construction of a Moran-type dam would result in a marked turbidity reduction. This could reduce the flow of organic material into the plume, which would likely deprive benthic organisms of a certain portion of their energy. This might be offset to some extent by the increased rate of primary productivity which the reduced turbidity would allow. The reduced turbidity might, however, lead to increased predation rates on young pink and chum salmon. Mortality of salmon in the early stages of their marine existence is already high (Parker, 1968, reported values of 59–77% in the first 40 days). An increase of mortality by an additional 10% as a result of improved visibility could reduce present sea survival of young salmon by as much as 45%.

Another probable effect of a high Moran-type dam would be the creation of nitrogen supersaturation in the river for an undetermined distance downstream. The extent of this problem is becoming increasingly evident from work on the Columbia River where serious mortalities of both adult and young are attributable to the effects of supersaturation (Beiningen and Ebel 1970). This supersaturation usually occurs in two ways. Water passing over a spillway entrains air which is forced into solution when the water enters the plunge basin, thus creating supersaturation. Nitrogen supersaturation could also be expected at some depth below the surface of the reservoir as is the case in lakes (Harvey 1967). Warming from the surface would result in supersaturation below perhaps 10 m, at which depths wind mixing is not likely to result in equilibration of the dissolved nitrogen with that in air. Consequently, water drawn from the hypolimnion passing through the turbines would also be supersaturated during the summer months. Fish both in the reservoir and downstream from the dam would be exposed to nitrogen supersaturated water. When the nitrogen comes out of solution within a fish, it creates emboli in the bloodstream and various tissues which can cause mortality or tissue necrosis. This can be expected to affect fish in a situation in which hydrostatic pressure is reduced, such as in a river below a dam or when a fish moves from nitrogen supersaturated hypolimnetic waters to the less saturated epilimnion. The distance downstream that supersaturated conditions would persist is unknown but is likely to be many miles (Anon. 1971a; Hughes 1973) in which case fish moving into Seton Creek or the Thompson River might be affected.

Construction of Moran Dam would result in many downstream changes that would probably reduce the size of salmon populations. It would also produce a number of changes upstream. The creation of a reservoir would dramatically reduce water velocities in the flooded regions of the river. Upstream and downstream migrants could not be expected to find their way through such a reservoir with reasonable speed, because a navigational cue would be largely eliminated. Losses of both adults and juveniles would be expected in the reservoir, as has occurred on the Columbia River.

Many other possible effects of a Moran-type dam could be cited and potential problems on which few data are available could be described. Likely the salmon populations upstream of a Moran-type dam could not be saved (Andrew and Geen 1960; Anon. 1971a; Geen 1972). Those stocks utilizing the lower areas of the Fraser River and tributaries of the lower river might also decline as a consequence of altered downstream conditions.

Proposals for development of hydroelectric power in British Columbia have often involved diversion of water from one drainage system to another. The possible consequences of diversions, which have been reviewed by Lindsey (1957), center around the introduction of organisms from the Yukon or MacKenzie systems to Pacific drainage basins. Two examples will serve to illustrate potential problems. Northern pike do not presently occur in the Fraser River system, but are found in the Peace River and its tributaries. Some proposed development schemes involve diversion of water from one of these systems to the other which would almost inevitably result in the invasion of the Fraser River by pike. This species, by virtue of its well-known piscivorous habits, could reduce the freshwater survival of juvenile salmon in the lakes and rivers of the Fraser River system. In addition, pike would probably serve as a vector of a parasite new to the Pacific slope. The tapeworm, *Triaenophorus crassus*, utilizes the pike as its definitive host. This parasite forms a cyst in the musculature of intermediate fish hosts (of which salmonids are an example), renders the flesh unattractive, and reduces its marketability.

The major hydroelectric developments in British Columbia are at present located on rivers that do not support anadromous salmonids — the Peace River, the upper parts of the Columbia River, and the Kootenay River (Fig. 1, 2).

The probable effects of construction of a 180 m high dam on the Peace River near Hudson Hope, B.C. on fish have been reviewed by Withler (1959). In addition to the conversion of a fast-flowing river to a large reservoir (1660 km^2), he predicted elimination of grayling populations and the likely development of whitefish and lake trout populations in the reservoir. The large reservoir will undoubtedly lead to a significant increase in fish production, though this will be minimized by the extensive annual drawdown. An increased sports fishing potential may have resulted from this development, although the failure to clear the lake margins prior to flooding has created an unsightly reservoir that is hazardous to boat travel. Downstream effects of this development are considered in detail in a later section of this review.

The Columbia River and its tributary, the Kootenay River, are the most extensively developed for hydroelectric power generation of any major river in Western Canada. The Columbia River in Canada has dams at Mica Creek and at the outlet of the Arrow Lakes, and a third one is proposed upstream of the Arrow Lakes near Revelstoke. The Kootenay River, dammed at Libby, Montana, creates a reservoir extending back into Canada (Fig. 2). Dams also exist on the Kootenay between Kootenay Lake and the Columbia River.

Probable effects of the Mica Dam and the Hugh Keenleyside Dam at the outlet of the Arrow Lakes have been considered by Peterson and Withler (1965b, c). In general, their predictions relative to the Mica development are in keeping with the effects of other projects in which a free-flowing river is dammed. The river fauna will be lost, access to spawning areas upstream of the dam will be blocked, productivity in the reservoir will be initially high but will eventually decline, and there will be low littoral productivity as a result of drawdown. Turbidity will decrease through settling of sediment in the reservoir (Peterson and Withler 1965c). Peterson and Withler were unable to define expected temperatures of the river downstream of the dam in anything but the most general terms. This is a reflection of the considerable variability in timing and magnitude of downstream discharge, coupled with the complex problem of predicting temperatures in reservoirs even when the discharge regime is known.

The increased storage on the Arrow Lakes resulting from construction of the Hugh Keenleyside Dam flooded approximately 160 km^2 of land. Peterson and Withler (1965b) anticipated changes

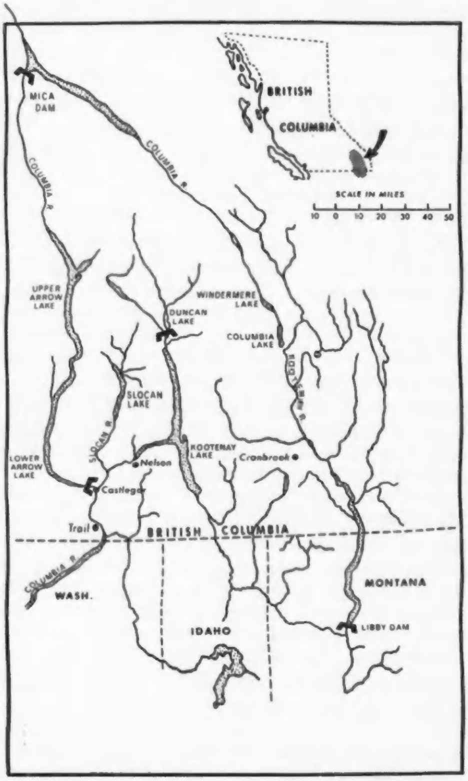


FIG. 2. Location of hydroelectric developments in the Kootenay region of British Columbia. Mica Dam on the Columbia River has created a large reservoir. The Columbia flows into the Arrow Lakes whose level is regulated by the Hugh Keenleyside Dam located at the lower end of the lakes near Castlegar and upstream from the confluence of the Columbia and Kootenay Rivers. Libby Dam in the State of Montana has flooded a portion of the Kootenay River and created a reservoir extending up into British Columbia. From Libby Dam the Kootenay River flows into Kootenay Lake and thence to the Columbia River. Duncan Dam serves to regulate discharges from Duncan Lake into Kootenay Lake. This figure is adapted from Whately (1972).

in the system, including increased drawdown, and changes in sedimentation, discharge, and temperature regimes. The anticipated effects of these changes include a decrease in growth rates of fish such as rainbow trout, which feed on littoral organisms, and a decrease in population size through loss of stream spawning grounds. Other species can also be expected to decline as a result of loss of spawning grounds.

These preimpoundment studies on the Peace and Mica developments have not been followed by any major postimpoundment studies, which is not surprising in view of the present limited recreational use of these areas. Although some work is currently underway on Arrow Lake to evaluate consequences of the proposed development on the Columbia River above Revelstoke, there are few local data on which to base predictions of the effects of future hydroelectric developments, and it will continue to be necessary to refer to studies in Scandinavian countries or the United States. This may be adequate for predicting some of the effects of impoundments, such as postimpoundment nutrient increase of reservoir waters for a few years, decreased littoral production, and so forth. However, there are few data on which to predict changes in temperature that could be expected downstream from the dams. This is not surprising, given the limited knowledge of the behavior of density currents in reservoirs and the distance downstream in a reservoir that stratification sets in, given a large volume inflow. Nor are many data available on effects of hydroelectric developments on growth and population dynamics of local fish species.

The probable effects of hydroelectric developments on the Kootenay River and Duncan Lake have been assessed and are the subject of some postimpoundment investigation. The Kootenay River has been dammed at Libby, Montana, 350 km upstream from its confluence with the Columbia River (Fig. 2). Libby Dam, a high-head dam, has created a 144 km long reservoir which extends 67 km into Canada at full pool elevation. This project has been the subject of considerable controversy, as it has major sociological and ecological implications. Flooding associated with this development has resulted in loss of farm lands and a reduction in winter range of large ungulates.

The predicted effects of the Libby Dam on fish are rather typical of those developments in which a river is flooded (Whately 1972). Extensive drawdown (up to 52 m), dessication and freezing (or both) of animals in the exposed littoral area during winter, increased sedimentation in the reservoir with a resultant increase in downstream clarity, and changed flow and temperature regimes below Libby Dam have been predicted. The temperature regime is, as usual, difficult to predict, although Whately (1972) expects that summer stratification will develop and that withdrawal of water for power generation from subsurface levels will lead to reduced downstream temperatures.

Changes in the chemical composition of water of the reservoir are expected to include the usual increases in TDS associated with leaching of the flooded terrain and breakdown of terrestial plant material. Chemical composition will be further affected by the inflow of chemical wastes from an upstream smelter, fertilizer plant, and pulpmill. The combined effect on Libby Reservoir of these chemical discharges might be one of increased fertility which could lead to seasonal algal blooms and perhaps a seasonal decline in oxygen in deeper waters, particularly if there is an appreciable deposition of pulpmill fiber in the reservoir.

Flooding of the Kootenay River will eliminate a whitefish population which is the basis of a winter fishery. This will probably be replaced by a lake cutthroat (*Salmo clarki*) trout fishery.

Additional regulation of the flow into Kootenay Lake has resulted from construction of a storage dam on Duncan Lake which drains to Kootenay Lake via the Duncan River (Fig. 1, 2). Peterson and Withler (1965a) predicted that this development would result in a summer reduction of downstream temperatures, a loss of spawning areas through flooding of streams, and extensive drawdown. They concluded that plankton-feeding fishes, such as kokanee, should benefit as volume and initial productivity would increase. Benthic-feeding trout would be expected to show decreased growth rates as a result of reduced food abundance (a consequence of dessication and smothering with sediments). Productivity of the Duncan River would be reduced by decreased summer temperatures and increased as a result of increased water clarity. The net effect is difficult to predict.

Changes in physical and chemical features of both the Kootenay and Duncan rivers resulting from the developments just described could have profound downstream effects on Kootenay Lake (Northcote 1973; Peterson and Withler 1965a; Andrusak 1972). Turbidity and summer temperatures of both these major inflows will decrease as will phosphorus load in the Kootenay River below the Libby Dam. The reduced turbidity will result in increased primary production, which may be only partially countered by the decreased phosphorus load and reduced temperature. Both Whately (1972) and Peterson and Withler (1965a) suggest that the changes in temperatures, turbidity, and flow regimes of the Kootenay and Duncan rivers are likely to modify current patterns in Kootenay Lake, which might affect lake productivity and homing ability of adult salmonids. For example, reduced turbidity may influence the existence of density currents within the lake. Currents such as these may serve as important guides during the streamward migration of maturing salmonids. Some changes in distribution of large rainbow trout within Kootenay Lake have already been noted since the closure of the Duncan Dam in 1967, although cause and effect has not been demonstrated. Andrusak (1972) reported a downward trend in numbers of large rainbow trout since the mid-1960s in the North Arm of Kootenay Lake; the rainbow trout fishery in the South Arm has vastly improved over the same period. Andrusak has suggested that these distribution changes may be the result of changed current patterns associated with altered temperature–turbidity–discharge regimes of the Duncan River. Further study is evidently warranted, given the recent closure of Libby Dam and the great importance of Kootenay Lake salmonid stocks for sports fishing.

Alberta

Local effects of damming the Peace River in British Columbia have been described above. Downstream effects of this development have had their major impact in Alberta and are reviewed at this point.

The construction of the Bennett Dam on the Peace River has resulted in regulated average discharge of about 1000 m^3/s compared with a predevelopment range of flows from 140–8680 m^3/s (Anon. 1971b). This regulation of flow has had important effects on the Peace–Athabasca Delta, a 3,776 km^2 area at the west end of Lake Athabasca. Both the Peace and Athabasca rivers flow in a north and easterly direction from their origins in the Rocky Mountains 1100–1300 km towards Lake Athabasca, which straddles the Alberta–Saskatchewan border just south of latitude 59°N (Fig. 3). The Athabasca River flows across the delta and into Athabasca Lake through a number of channels. The outflow is primarily through the Rivière des Rochers, which joins the Peace River north of the delta to form the Slave River (Fig. 4).

Prior to the 1968 closure of the Bennett Dam, the level of the Peace River for a period of 3 wk during the spring flood was typically higher than that in Lake Athabasca. This resulted in a blockage of flow from Lake Athabasca, which in most years led to an increase in lake elevation to a level at which it flooded over the delta; but this did not occur invariably each spring. In those years when Peace River levels were low, water flowed rapidly from Lake Athabasca and little flooding of the delta occurred. With the advent of regulation, spring Peace River flows are invariably low and delta flooding is limited. This has already led to a number of dramatic changes in plant and animal communities of the delta.

The delta, an area in the early stages of plant succession, is dominated by sedges (*Carex atherodes*), reedgrass (*Calamagrostis canadensis*), many groups of animals including bison and muskrat, and many

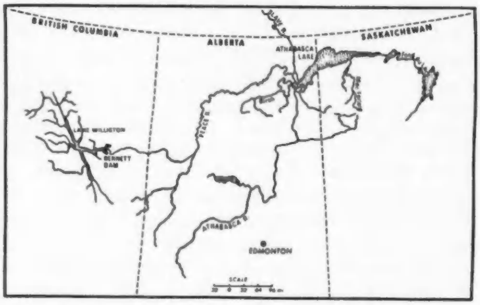


FIG. 3. Location of Lake Athabasca, the Peace and Athabasca rivers, and the W.A.C. Bennett Dam on the Peace River. Adapted from Kellerhals (1971).

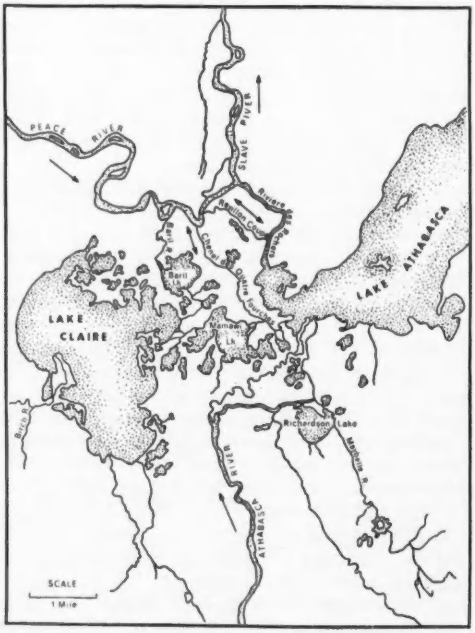


FIG. 4. The Peace–Athabasca Delta indicating the location and direction of flow of the principal rivers of the area. Adapted from Kellerhals (1971).

species of waterfowl (Dirschl 1971). In the absence of spring flooding, plant succession proceeds quickly to the point where willow communities replace the sedge and grass meadows. Loss of these meadows is expected to significantly reduce the delta's carrying capacity for bison (Dirschl 1971).

The muskrat, a semiaquatic mammal and traditional mainstay of delta trappers, is also dependent on the marshes in which they construct their houses of emergent vegetation. Muskrat populations have declined dramatically in recent years, apparently because the marshes that previously supported muskrat houses had become too shallow. The spring flooding produced by high water in the Peace River is required to ensure a sufficient depth of water in the marsh to permit the muskrat to overwinter successfully (Anon. 1973b; Dirschl 1971).

The delta is also an important breeding and staging area for waterfowl. Over 600,000 young ducks were produced on the delta in 1972. Waterfowl production will probably decline if water levels are permitted to remain low. These low levels will reduce the number of nests lost to flooding and improve the hatches. However, the low water levels will reduce the nesting areas available (Anon. 1973b). Brood survival may be jeopardized by the disappearance of emergent vegetation that protects broods from predators (Dirschl 1971).

Initial studies have also been conducted to assess effects of the changed water regime on fish populations of the area. Lake trout, walleye, goldeye (*Hiodon alosoides*), northern pike, and lake whitefish are all taken in quantity from Lake Athabasca, the first three being the most important. Richardson Lake (Fig. 4) is apparently a major spring spawning area for walleye from Lake Athabasca. In years of low water Lake Richardson could freeze to the bottom and thereby prevent walleye from entering the lake or the Maybelle River to spawn until after ice break-up, leading to a serious delay of spawning. Young walleye could also be frozen in the winter ice of Lake Richardson or be killed by high summer temperatures that would result in the shallow waters if no flooding occurred (Bidgood 1971).

Goldeye spawn in Lake Mamawi and Lake Claire. Water levels are still adequate to permit migration into these areas. The drop of about 0.5 m in Lake Athabasca is not regarded as having a major impact on fall spawning lake trout. However, it has been suggested (Peace–Athabasca Delta Committee 1970) that cisco (*Coregonus artedii*) spawning areas on the shores of Lake Athabasca are now exposed during winter. The eventual collapse of populations of harvestable fish (walleye, pike, and lake trout) has been suggested as a likely consequence if there is a decline in the cisco population, as they are the basic food supply for the carnivorous species.

Changes in the delta and reduction of levels of Lake Athabasca are of considerable consequence because they impair ship navigation, reduce the fur resource on which native people depend, will inevitably affect fish, waterfowl, and ungulate populations, and will result in changes in a whole way of life. If these problems were envisaged prior to damming the Peace River, they received little publicity and no obvious consideration of ways to minimize the effects.

Remedial measures are necessary if these ecological changes are to be reversed and a way of life maintained. Some ideas have been proposed, all of which involve raising spring water levels in Lake Athabasca so that flooding of the delta occurs annually (Anon. 1973b). A low temporary dam was completed across the Chenal des Quatre Fourches at the outlet of Mamawi Lake in 1971 (Fig. 4). This raised the summer levels of lakes Claire and Mamawi and adjacent ponds and perched basins. However, the key to the problem still lies in increasing water levels in Lake Athabasca. Construction of a permanent fixed-weir dam on the Riviere des Rochers has been recommended (M. Paetz personal communication). This would ensure annual flooding of much of the delta and maintenance of higher water levels in Lake Athabasca — a return to earlier conditions. Continuing rapid action is necessary to restore the delta to conditions that prevailed prior to construction of the Peace River dam.

Obviously development of the Peace River should not have been permitted without a prior assessment of its impact and a plan for minimizing the consequences. Such assessments are now usually considered in deciding whether a project should proceed. However, despite heightened public awareness of biological, sociological, and economic consequences of hydroelectric developments, not all developers and government agencies carefully consider new hydroelectric schemes and air benefits and costs in a public forum. The Churchill–Nelson project in Manitoba and the James Bay development in Quebec are notable current examples in which provincial governments have not requested extensive impact studies before proceeding with highly controversial developments. Although development of the Peace River may have been reasonable under the circumstances, public pressure is going to require that such decisions be reached in the future only after interested groups have presented their views and have participated in the decision-making process.

Some of the most intensive work in Canada on effects of hydroelectric development on aquatic ecosystems has been conducted in the Rocky Mountain lakes and rivers of Alberta. Studies in the Banff-Kananaskis area were initiated by D. S. Rawson in the 1930s and have been continued from time to time since then. The bulk of the work has centered on the Bow River and its tributaries; it rises in the Rocky Mountains west of Calgary and flows east to join the South Saskatchewan River.

Lake Minnewanka, largest of the Bow headwater lakes, has been investigated since 1936. Cuerrier (1954) noted that the physical and chemical characteristics of this lake changed little following construction of a first dam in 1911–12, and of a second one in 1941, which raised the original lake level a total of 23 m. The plankton had altered little, if any, since the first studies (Miller and Paetz 1959; Rawson 1942). However, the bottom fauna had changed dramatically (Rawson 1942; Cuerrier 1954). In 1941, the first year of flooding associated with construction of the higher dam, the average weight of benthic organisms dropped to 0.64 kg/hectare from the 1.2 kg/hectare recorded in 1936. A further decline in 1943 was followed by increased standing crops in 1947 and 1951 (Cuerrier 1954). These changes in biomass were reflected in a shift in bottom fauna composition. Chironomids increased from 52.5% by number in 1936 to more than 90% in 1943 and subsequent years. Sphaeriids declined from 38.6% in 1936 to less than 5% by 1943. Insect larvae, other than chironomids, had largely disappeared.

Cuerrier (1954) also reported a downward shift in the average size of lake trout following the 1941 flooding. Fish 40–50 cm, comprising 38.9% of the net catch in 1941, decreased to 6.7% by 1947. Fish 20–30 cm showed a corresponding increase in abundance, a change associated with a shift in diet of the trout. In 1943, 53% of the stomachs of fish 25–35 cm contained fish; none did in 1952. The percentage occurrence of fish in stomachs of large trout was high in both years. Cuerrier (1954) suggested that immature trout (< 35 cm) were spatially separated from Rocky Mountain whitefish, their prey prior to flooding. Whitefish were primarily in surface waters whereas trout were in deeper waters. Under preimpoundment conditions, trout 4–6 yr of age began to feed on fish. This did not happen after flooding, with the result that growth and survival of trout declined to the point that few large fish remained. Cuerrier (1954) suggested that common lake whitefish be planted, because it inhabits the same parts of a lake as lake trout and could therefore serve as food source. Eyed whitefish eggs were planted in 1953. However, this endeavor apparently did not succeed.

The Kananaskis River, now extensively developed for hydroelectric power generation, has been the subject of thorough study and provides the most carefully documented description in Canada of the changes which follow flooding. The Kananaskis River drains into the Bow River 64 km west of Calgary. The 84-km river drops 404 m from Upper Kananaskis Lake to the river mouth. Dams have been built on Upper Kananaskis Lake (1936, 1942), on Lower Kananaskis Lake (1954), and on the lower Kananaskis River (1947), forming Barrier Reservoir. The Kananaskis River flows from the Barrier Reservoir into the Kananaskis Reservoir on the Bow River.

Effects of flooding the Kananaskis River to form the Barrier Reservoir were first assessed by Nursall (1952). Flushing rate was relatively high (11.4 times per year) and the plankton scarce in number and variety. The early development of bottom fauna in the reservoir was marked by miscellaneous survivors of the river fauna. *Pentapedilum* was the first chironomid to become established. Members of the chironomid subfamilies Chironominae and Tanypodinae succeeded in that order. *Chironomus*, an eutrophy-typical form, flourished under the relatively eutrophic conditions presented by leaf litter on the reservoir bottom. Silt associated with the spring runoff in 1948 completely buried the litter and the oligotrophy-typical *Tanytarsus* became dominant, a reflection of the more severe environment.

Fillion (1967) noted that pisidia, present in the two upstream reservoirs, had invaded the Barrier Reservoir. All groups of benthic organisms had their maximum abundance below the zone subject to drawdown. An analysis of the distribution of fauna along the length of Barrier Reservoir indicated maximum abundance some distance down-reservoir. The reservoir region above the zone of maximum abundance is subject to drawdown and consequently had a low standing crop. The region down-reservoir from the zone of maximum abundance also had a lower standing crop, which Fillion attributed to a reduced quantity of allochthonous organic matter in the lower part of the reservoir.

The consequences of flooding Upper and Lower Kananaskis Lakes have been reviewed by a number of workers (Miller and Paetz 1959; Fillion 1967; Radford 1972). The changes are those expected under conditions of regulation. Standing crops of plankton were little affected. Weight of benthic organisms decreased, attributable primarily to decrease in abundance of pisidia. Chironomids increased to dominate the benthic fauna, a feature characteristic of many reservoirs experiencing significant drawdown. *Gammarus*, an important food for salmonids, virtually disappeared.

Radford and Hartland-Rowe (1971) have examined the bottom fauna and invertebrate drift in the Kananaskis River and one of its unregulated tributaries, Lusk Creek. They noted that biomass was lower in the Kananaskis River than in Lusk Creek, or in several other streams in North America. Low standing crop was attributed to the extremes of river discharge. The Kananaskis River biomass was made up primarily of torrential forms. The larger biomass of organisms in Lusk Creek was more diverse, a fact attributed to greater stability of conditions in Lusk Creek.

Radford and Hartland-Rowe (1971) also showed that reductions in discharge led to increased drift. It was presumed, as shown in other studies, that drift also increased as discharge increased. They also indicated that tributary streams contribute a significant amount of biomass to a parent stream by way of invertebrate drift.

Effects of developments on the Kananaskis River on fish populations have been reviewed by Nelson (1965), Miller and Paetz (1959), and Radford (1972). Dolly Varden (*Salvelinus malma*), rainbow trout, and cutthroat trout have all largely disappeared, a function of loss of spawning areas through either flooding or drying, decreases in benthic food organisms, and, for trout at least, the result of lowered summer temperature in the river below Lower Kananaskis Reservoir (Radford 1972). Longnose suckers (*Catostomus catostomus*) also disappeared, perhaps because of loss of stream spawning areas (Miller and Paetz 1959), and were replaced by a species of lake-spawning sucker. Nelson (1965) questioned this explanation of the longnose sucker decline as similar trends have occurred in adjacent areas in which the environment has been relatively stable; he felt that changes in the physicochemical environment and invertebrate fauna in the Kananaskis system reservoirs appeared to be secondary to interaction among fish in causing the changes in species abundance and distribution. The effects of these hydroelectric developments are in this case masked by the planting of several species of fish over a period of years.

Saskatchewan and Manitoba

Changes produced by hydroelectric developments in Saskatchewan and Manitoba have thus far been relatively little studied.

There are two major developments in Saskatchewan, on the Saskatchewan River system which drains into Lake Winnipeg in Manitoba. The construction of Gardiner Dam, located on the South Saskatchewan River south of Saskatoon, has created Diefenbaker Lake, a large reservoir serving both the irrigation and hydroelectric needs of the area. Further downstream on the Saskatchewan River the Squaw Rapids Dam has created Tobin Lake, the shallow reservoir that has resulted from development of this run-of-the-river dam.

Hypolimnetic discharge from Diefenbaker Lake results in decreased summer and increased winter temperatures. Lehmkuhl (1972) showed a marked reduction in macroinvertebrates as far as 112 km downstream. Nineteen species of ephemeropterans were found in the control area above the reservoir. None were observed immediately below the dam, and only seven species were collected 112 km downstream. Diversity and abundance of all invertebrates increased with distance downstream from the dam. All physical and chemical factors were nearly constant from the dam to the lowest station except temperature, which had lower summer maxima and higher winter minima below the dam than at the control stations. Lehmkuhl (1972) concluded that the absence of ephemeropterans was related to the altered temperature regime. The low temperatures in winter required to break diapause and stimulate egg hatching were absent. Sufficiently high summer temperatures were apparently lacking, with the result that nymphs did not reach maturity. The thermal requirements for development were met at the control stations but not in the 112 km from Gardiner Dam to Saskatoon. Lehmkuhl believes that the temperature changes have also eliminated nonephemeropteran invertebrates.

The influence of hypolimnetic discharge on downstream populations has received too little consideration, although it is a characteristic of many developments. Changes of the type described by Lehmkuhl are relatively subtle and not easily predicted given the current state of knowledge, but are clearly of the type that could lead to profound changes in fish populations.

The Saskatchewan River empties into Cedar Lake, Manitoba, which is now the head pond for the Grand Rapids power plant, located just upstream from Lake Winnipeg. Cedar Lake was the subject of a preimpoundment study in the early 1960s and a postimpoundment investigation in 1973. This, plus work on Reindeer Lake in Saskatchewan, represents the first attempts to evaluate effects of hydroelectric development on aquatic ecosystems in Precambrian Shield lakes and rivers, and the results will be interesting. Other than the Cedar Lake study, no major systematic attempt has been made to assess the impact of older hydroelectric developments in Manitoba.

One of the most controversial hydroelectric projects in Canada is currently under construction in Northern Manitoba. The Nelson River, which flows from Lake Winnipeg to Hudson Bay, has a series of dams either in existence or contemplated within the next 20 yr. Maximum power is to be generated at these downstream plants by regulating flow from Lake Winnipeg for release during periods of low flow. A control structure is being built to regulate Lake Winnipeg elevations between 213.3 and 214.5 m. This will undoubtedly affect beaches and marshes and have related implications to recreation and wildlife uses, although these have yet to be described in detail.

Most of the controversy related to this development centers on the plan to divert the waters of the Churchill River to the Nelson River system. Although these rivers are several hundred miles apart, a low height of land separates the Churchill at South Indian Lake from nearby tributaries of the Nelson system. Present plans call for the construction of a dam at the outlet of South Indian Lake to divert water via the Rat and Burntwood rivers to the Nelson River (Newbury and Malaher 1973); this diversion will reduce the downstream flow of the Churchill from an annual mean of 1000 m^3/s to summer and winter minima of 14 and 42 m^3/s, respectively. The esthetic qualities of the river will be altered significantly by the reduced flows (Newbury and Malaher 1973).

The level of water in South Indian Lake will be increased approximately 3 m and will flood an area of 540 km^2. Considerable socioeconomic impact is anticipated, including relocation of an Indian village.

Diversion of Churchill River water along the Rat–Burntwood diversion route will significantly alter the characteristics of the system. Flows will be increased from 115 m^3/s to 1000 m^3/s. The Notigi Lake control structure on the Rat River system will flood an additional 400 km^2 of land. Additional flooding can be expected as additional generating sites are developed along the diversion route (I. Dickson personal communication).

Steps are being taken to minimize the impact of the diversion on the lower part of the Churchill River system. A minimum downstream discharge will be required and fish ladders may be provided at points of difficult passage (K. Doan personal communication). Some shoreline clearing around South Indian Lake will be required. Major changes can be expected in fish populations in the Churchill as well as in rivers and lakes which are flooded out.

In its planning stages, there was considerable opposition to the diversion scheme. Not only was the development proceeding with little, if any, appreciation of the significance of the changes which would result, but a community of Indians on South Indian Lake was to be flooded out when the elevation of the lake was increased. Despite these concerns, the project is proceeding.

A major biological study has now been initiated by the Canadian and Manitoba governments. It will undoubtedly provide the great wealth of information that should have been considered before the project was authorized. Hopefully some postimpoundment study will also be conducted.

The decision to proceed with the Churchill–Nelson project seems to have been made by applying only those criteria traditionally employed — cost of power produced and predicted future need for power either locally or for export, based on some assumed rate of load growth. There seems to have been little awareness, before deciding to proceed, that social or ecological considerations might outweigh the benefits of development.

This approach to decision-making on matters relating to natural resources is clearly a continuation of past habits, which are now deemed unacceptable in many quarters. The only satisfactory approach is that in which all those affected by a hydroelectric development, of which the Churchill–Nelson is a prime example, have the opportunity to comment formally and knowledgeably to a government decision-making group, in advance of the critical decisions. Knowledgeable comment can stem only from a solid foundation of sociological, ecological, and economic data which require considerable effort and time to amass and interpret. A similar lack of opportunity for public involvement and an absence of background biological and sociological data seems to characterize Quebec's James Bay development. A broad review of the costs and benefits of both these developments may have shown that maximum benefit for the most people might result from permitting these developments to proceed. However, this broad look has apparently never been adequately taken, and the projects commence under the suspicion that economic gain is placed before all other considerations.

Yukon and Northwest Territories

The vast area of Northern Canada encompassed by the Yukon and Northwest Territories is characterized by a small population concentrated in relatively few centers. The small and scattered populations and the great distances involved have meant that hydroelectric developments are relatively small and designed to meet local needs rather than for transmission to distant population centers. The large lakes, which might serve as major reservoirs, have not been developed for hydroelectric power, if for no other reason than that the demand for large quantities of electricity does not exist there now.

The majority of hydroelectric developments have taken place with little or no prior assessment of their ecological implications. This is perhaps not surprising considering the remoteness of the area and the vast areas of water in Northern Canada. However, as in most areas of Canada, attitudes are changing and some attention is now being paid to the likely consequences of each development before deciding whether the project should proceed.

The major hydroelectric development in the Yukon is on the Yukon River just above Whitehorse. A spillway dam raised the elevation of the river about 14 m. Fish collection and passage facilities were installed to ensure that runs of chinook salmon and other fish were able to move up around the dam (Gordon et al. 1960); it seems to be functioning well.

More recently the Northern Canada Power Commission was authorized to begin construction of an hydroelectric generating facility on the Aishihik River system. It involves a dam on the outlet of Aishihik Lake and a second dam downstream on the much smaller Canyon Lake which would provide the water supply for a downstream powerhouse.

Fisheries problems associated with this development have recently been reviewed (Anon. 1973a). Apparently the flooding and extensive drawdown (or both) associated with this project would have adverse effects on sport and commercial fish species. Drawdown of Aishihik Lake below present levels could lead to erosion and general deterioration of tributary rivers and streams, many of which are presently used for spawning and rearing. Drawdown could also result in tributary streams eroding their relatively productive deltas, which probably serve as spawning and rearing areas.

Aishihik Lake is an oligotrophic body of water in which greatest abundance of littoral organisms occurs at depths between 2–8 m. The insects and gastropods found in the littoral area are a major food component of lake trout and whitefish. Drawdown will have to be limited if the littoral fauna is not to be seriously reduced.

To achieve the necessary water storage for economic power development, some flooding or additional drawdown will probably be necessary. This storage could be achieved by modest increase in lake surface elevation and drawdown of 1–2 m below present minimum elevations. Careful development of this sort might minimize the impact on the environment of important fish species in the lake.

Extensive drawdown could readily have great significance to the fall-spawning species such as lake trout and whitefish whose eggs overwinter in the littoral area. Exposure of incubating eggs would inevitably lead to a decline of these species. In view of the possible loss of overwintering eggs, the likelihood of erosion of streams, and of loss of littoral food supplies, the Fisheries Service tentatively concluded that flooding would be less damaging than extensive drawdown from present levels (Anon. 1973a).

Thus far, there have been no detailed assessments of the ecological effects of hydroelectric developments in the Northwest Territories, although the consequences of several projects in the planning stage are being considered. Careful evaluation of the effects of any of these developments would be highly desirable, particularly as the frequency of these hydroelectric developments will likely increase, and as the biology of many important aquatic species in these arctic waters is poorly understood.

Conclusions

I have reviewed some of the effects of existing or proposed hydroelectric developments on the lakes and rivers of western Canada. Early in the preparation of this review it became apparent that most attention has thus far been directed to assessing probable effects of proposed developments. Relatively little effort has been put into postdevelopment assessment of changes. In retrospect, it is probably not surprising that this should be the case. Government management agencies are invariably understaffed and can often do little else than supplement a modest amount of field work with information from the existing literature and their own experience in making predictions on the consequences of hydroelectric development. Sometimes this approach seems to be adequate, particularly where a fishery resource is little used; however, it is probably inadequate when dealing with fish populations of recreational or commercial importance. Effective protection and management of important resources will require a solid base of information on the biology of the species involved. At present these data are generally inadequate. One only has to attempt to predict consequences of reduced turbidity on predator–prey interactions downstream from a dam to appreciate the limitation of much of the available data.

The majority of postimpoundment studies conducted to date in western Canada have been on reservoirs or flooded lakes rather than on rivers downstream from hydroelectric developments. The results tend to confirm those of studies from other parts of the world. Littoral production is usually low, a reflection of the effects of drawdown, and plankton production and water chemistry are little affected although an initial increase in TDS and production can be expected. Growth rates of fish feeding on littoral organisms are frequently reduced, and the relative abundance of fish and their food organisms is frequently altered. Thus, there are sufficient data with which to make general predictions of the effects on fish invertebrates of creation of a reservoir from a lake or river. However, often too few data are available to permit prediction of the vertical or horizontal temperature regimes of a reservoir. This is particularly true in reservoirs receiving a large inflow of cold, turbid water. The point along the reservoir at which stratification will occur and the behavior of density currents are not readily predictable, although of considerable biological significance both in the reservoir and downstream.

There is a serious lack of information on downstream effects of hydroelectric projects. Altered temperature and flow regimes, reduced turbidity, and gas supersaturation are well-documented changes associated with many hydroelectric developments. Major changes in downstream populations of aquatic organisms could readily result from any of these alterations. Indeed, many of the problems presently being encountered at hydroelectric developments relate to downstream changes. The consequences on the Peace–Athabasca Delta of damming the Peace River, the possible effects of regulation of flow into Kootenay Lake from Duncan and Kootenay rivers, and the impact of any high dam on the Fraser River have all been cited as examples.

We need to recognize that the effects of these changes are not readily predictable from the present data base. This area requires most urgent attention. The recent work of Lehmkuhl (1972) points to the type of downstream changes which can be expected and can be readily visualized as having important effects on resident or migratory fish populations.

Acknowledgments

Numerous persons have assisted by bringing to my attention published and unpublished reports on the effects of hydroelectric developments on lakes and rivers in western Canada. Their assistance is gratefully acknowledged.

Andrew, F. J., and G. H. Geen. 1960. Sockeye and pink salmon production in relation to proposed dams in the Fraser River system. Int. Pac. Salmon Fish. Comm. Bull. 11: 259 p.

Andrusak, H. 1972. Kootenay Lake sport fishery 1970–71. B.C. Fish Wildl. Branch. 52 p. (mimeo.)

Anon. 1971a. Fisheries problems related to Moran Dam on the Fraser River. Dep. Environ. Fish. Serv., Int. Pac. Salmon Fish. Comm. 206 p.

1971b. Appendix: Some data and references on the Portage Mountain development (W.A.C. Bennett Dam), p. 145–151. *In* E. R. Reinelt et al. [ed.] Proc. of the Peace–Athabasca Delta Symp., Univ. Alberta, Edmonton, Alta.

1973a. Fisheries problems associated with the proposed Aishihik River power development. Interim Report. Dep. Environ. Fish. Serv., Vancouver, B.C. 45 p.

1973b. The Peace–Athabasca delta. A Canadian resource. 1972. Summary report of the Peace–Athabasca Delta Project Group. 144 p.

Beiningen, K. T., and W. F. Ebel. 1970. Effects of John Day Dam on dissolved nitrogen concentrations and salmon in the Columbia River, 1968. Trans. Am. Fish. Soc. 99: 664–671.

Bidgood, B. F. 1971. Ecology of walleyes *Stizostedion v. vitreum*, in the Richardson Lake–Lake Athabasca complex, p. 187–203. *In* E. R. Reinelt et al. [ed.] Proc. of the Peace–Athabasca Delta Symp., Univ. Alberta, Edmonton, Alta.

Brett, J. R. 1957. Salmon research and hydroelectric power development. Bull. Fish. Res. Board Can. 114: 26 p.

Carl, G. C. 1937. Preliminary survey of Campbell Lake. Pac. Biol. Sta., Nanaimo, B.C. (unpublished rep.)

Cuerrier, J.-P. 1954. The history of Lake Minnewanka with reference to the reaction of lake trout to artificial changes in environment. Canadian Fish Culturist 15: 1–9.

Dirschl, H. J. 1971. Ecological effects of recent low water levels in the Peace–Athabasca delta, p. 174–186. *In* E. R. Reinelt et al. [ed.] Proc. of the Peace–Athabasca Delta Symp., Univ. Alberta, Edmonton, Alta.

Efford, I. E., and B. M. Smith [ed.] 1972. Energy and the environment. H. R. MacMillan Lectures in Fisheries, Univ. British Columbia, Vancouver, B.C. 220 p.

Fillion, D. B. 1967. The abundance and distribution of benthic fauna of three mountain reservoirs on the Kananaskis River in Alberta. J. Appl. Ecol. 4: 1–11.

Geen, G. H. 1972. Downstream effects of hydroelectric development at Moran Canyon. B.C. Energy Board Rep. Appendix 1-A, Annex I, Appendix ii: 29 p.

Geen, G. H., and F. J. Andrew. 1961. Limnological changes in Seton Lake resulting from hydroelectric diversions. Int. Pac. Salmon Fish. Comm. Prog. Rep. 8: 76 p.

Gordon, R. N., R. A. Crouter, and J. S. Nelson. 1960. The fish facilities at the Whitehorse Rapids power development, Yukon Territory. Canadian Fish Culturist 27: 43–56.

Harvey, H. H. 1967. Supersaturation of lake water with a precaution to hatchery usage. Trans. Am. Fish. Soc. 96: 194–201.

Hughes, S. 1973. Summary report. Supersaturation levels in Kootenay River downstream from Libby Dam and in the Columbia River south of the border. B.C. Fish Wildl. Branch. 5 p. (mimeo.)

Idler, D. R., and W. A. Clemens. 1959. The energy expenditures of Fraser River sockeye salmon during the spawning migration to Chilko and Stuart Lakes. Int. Pac. Salmon Fish. Comm. Prog. Rep. 6: 80 p.

Kellerhals, R. 1971. Factors controlling the level of Lake Athabasca, p. 57–109. *In* E. R. Reinelt et al. [ed.] Proc. of the Peace–Athabasca Delta Symp., Univ. Alberta, Edmonton, Alta.

Larkin, P. A. [ed.] 1958. The investigation of fish-power problems. H. R. MacMillan Lectures in Fisheries, Univ. British Columbia, Vancouver, B.C. 111 p.

Larkin, P. A., et al. 1959. The effects on fresh water fisheries of man-made activities in British Columbia. Canadian Fish Culturist 25: 27–59.

Lehmkuhl, D. M. 1972. Change in thermal regime as a cause of reduction of benthic fauna downstream of a reservoir. J. Fish. Res. Board Can. 29: 1329–1332.

Lindsey, C. C. 1957. Possible effects of water diversions on fish distribution in British Columbia. J. Fish. Res. Board Can. 14: 651–668.

Lucas, K. C. 1960. The Robertson Creek spawning channel. Canadian Fish Culturist 27: 3–23.

MacKinnon, D. 1960. A successful transplant of salmon eggs in the Robertson Creek spawning channel. Canadian Fish Culturist 27: 25–31.

MacKinnon, D., L. Edgeworth, and R. E. McLaren. 1961. An assessment of Jones Creek spawning channel. Canadian Fish Culturist 30: 3–14.

McMynn, R. G., and P. A. Larkin. 1953. The effects on fisheries of present and future water utilization in the Campbell River drainage area. B.C. Game Comm. Manage. Publ. 2: 61 p.

Mead, R. W., and W. L. Woodall. 1968. Comparison of sockeye salmon fry produced by hatcheries, artificial channels and natural spawning areas. Int. Pac. Salmon Fish. Comm. Prog. Rep. 20: 41 p.

Miller, R. B., and M. J. Paetz. 1959. The effects of power, irrigation, and stock water developments on the fisheries of the South Saskatchewan River. Canadian Fish Culturist 25: 13–26.

Nelson, J. S. 1965. Effects of fish introductions and hydroelectric development on fishes in the Kananaskis River system, Alberta. J. Fish. Res. Board Can. 22: 721–753.

Newbury, R., and G. Malaher. 1973. The destruction of Manitoba's last great river. Can. Nat. Fed. Spec. Publ. 2: 24 p.

Northcote, T. G. 1973. Some impacts of man on Kootenay Lake and its salmonoids. Great Lakes Fish. Comm. Tech. Rep. 25: 46 p.

Northcote, T. G., and P. A. Larkin. 1963. Western Canada, p. 451–485. *In* D. G. Frey [ed.] Limnology in North America.

Nursall, J. R. 1952. The early development of a bottom fauna in a new power reservoir in the Rocky Mountains of Alberta. Can. J. Zool. 30: 387–409.

Parker, R. R. 1968. Marine mortality schedules of pink salmon of the Bella Coola River, Central British Columbia. J. Fish. Res. Board Can. 25: 757–794.

Parsons, T. R. 1972. The influence of the Fraser River on the productivity of the Strait of Georgia (with special reference to the construction of a Moran-type dam). B.C. Energy Board Rep. Appendix 1-A, Annex I, Appendix x: 48 p.

Peace–Athabasca Delta Committee. 1970. Death of a delta. Univ. Alberta, Edmonton, Alta. 19 p.

Peterson, G. R., and I. L. Withler. 1965a. Effects on fish and game species of development of Duncan Dam for hydro-electric purposes. B.C. Fish Wildl. Branch Manage. Publ. 8: 72 p.

1965b. Effects on fish and game species of development of Arrow Lakes Dam for hydro-electric purposes. B.C. Fish Wildl. Branch Manage. Publ. 9: 43 p.

1965c. Effects on fish and game species of development of Mica Dam for hydro-electric purposes. B.C. Fish Wildl. Branch Manage. Publ. 10: 67 p.

Radford, D. S. 1972. Some effects of hydroelectric power installations on aquatic invertebrates and fish in the Kananaskis River system. Alberta Conserv. Summer 1972: 19–21.

Radford, D. S., and R. Hartland-Rowe. 1971. A preliminary investigation of bottom fauna and invertebrate drift in an unregulated and a regulated stream in Alberta. J. Appl. Ecol. 8: 883–903.

Rawson, D. S. 1942. The effect of the 1941 power development on the fisheries of Lake Minnewanka, Banff. Natl. Parks Bur., Dep. Mines Resour., Ottawa. 26 p. (mimeo.)

Sinclair, D. C. 1965. The effects of water level changes on the limnology of two British Columbia coastal lakes, with particular reference to the bottom fauna. M.Sc. Thesis. Univ. British Columbia, Vancouver, B.C. 84 p.

Whately, M. R. 1972. Effects on fish in Kootenay River of construction of Libby Dam. B.C. Fish Wildl. Branch Fish. Manage. Rep. 65: 49 p.

Withler, I. L. 1959. Fisheries problems associated with development of the Peace River and its upper tributaries for hydro-electric purpose. B.C. Fish Wildl. Branch Fish. Manage. Rep. 31: 20 p.

Trout Production in Prairie Ponds[1]

G. H. LAWLER, L. A. SUNDE, AND J. WHITAKER

Department of the Environment, Fisheries and Marine Service
Freshwater Institute, Winnipeg, Man. R3T 2N6

LAWLER, G. H., L. A. SUNDE, AND J. WHITAKER. 1974. Trout production in prairie ponds. J. Fish. Res. Board Can. 31: 929–936.

Experimental plantings of rainbow trout (*Salmo gairdneri*) in prairie winterkill lakes commenced in 1968 to test the feasibility of their commercial production. These trials were highly successful and by 1970 a small but rapidly expanding trout farming industry had been established. Trout planted early in the spring as 5- to 8-cm long fingerlings grew to marketable size (200 g minimum), without supplementary feeding, in the 6-mo period of open water that prevails in this region. Recoveries as high as 86% of the fingerlings stocked have been achieved and the quality of the trout produced is usually excellent in flavor and color. These experiments are continuing to improve management techniques and to determine the long-term productive capacity of pothole lakes. Three serious problems — summerkill, muddy flavor, and harvest inefficiency — are also subjects of continuing investigations. Use of prairie winterkill lakes as nursery ponds for production of advanced fingerlings of walleye and whitefish for use in resource-enhancement programs has also been tested with considerable success.

LAWLER, G. H., L. A. SUNDE, AND J. WHITAKER. 1974. Trout production in prairie ponds. J. Fish. Res. Board Can. 31: 929–936.

Le peuplement expérimental de truites arc-en-ciel (*Salmo gairdneri*) dans les lacs des Prairies sujets à des mortalités hivernales a débuté en 1968 en vue de déterminer la possibilité d'une production à l'échelle commerciale. Ces essais ont été fort réussis, et déjà en 1970 il s'était établie une industrie, petite mais rapidement grandissante, d'élevage de truites. Des truites ensemencées au début du printemps comme alevins de 5 à 8 cm de longueur ont atteint une taille commerciale (minimum de 200 g), sans addition de nourriture, au cours de la période de 6 mois d'eau libre de glace qui prévaut dans cette région. On a récupéré jusqu'à 86% des alevins ensemencés, et la qualité des truites, sous le rapport de la saveur et de la couleur, est ordinairement excellente. Ces expériences se poursuivent en vue d'améliorer les méthodes d'aménagement et de déterminer la productivité à long terme des "marmites." Trois problèmes sérieux — mortalités estivales, goût de vase et inefficacité de la récolte — font l'objet de recherches continues. L'utilisation de ces mêmes lacs comme étangs d'alevinage dans la production d'alevins âgés de doré et de grand corégone destinés à des programmes d'augmentation de la ressource a été également essayée avec beaucoup de succès.

Accepted January 11, 1974

THE Canadian prairies contain hundreds of thousands of small, shallow, highly productive lakes and ponds. They occur in a vast area of mixed grass prairie, aspen parkland, and mixed forest (Fig. 1) and are underlain primarily by sedimentary deposits. Large numbers of waterfowl and fur bearers are produced in these waters, but few contain fish due to the regular occurrence of winterkill.

Sport fish stocking demonstrated the potential of these waters for production of fish, and in 1968 the Freshwater Institute commenced studying their feasibility as the resource base for a prairie trout farming industry. By 1969, the potential of these lakes for trout culture had been shown and production began in 1970. Rainbow trout (*Salmo gairdneri*) of exceptional quality had been grown from fingerlings (3–4 g) to marketable size (over 200-g round weight) in one summer without supplementary feeding and recoveries of up to 86% of fingerlings stocked had been achieved. Research on the extensive culture of rainbow trout has continued and management techniques have been established and refined. In the private sector, upward of 1500 individuals are presently rearing

---

[1] This paper, part of a special issue that comprises a comprehensive review of Limnology in Canada, was prepared to mark the 19th Congress of the International Association of Limnology (SIL), in Winnipeg, Man., during August 1974.

Printed in Canada (J3277)

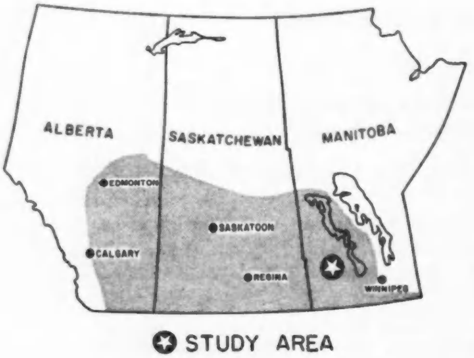


Fig. 1. The Prairie Provinces of Canada. Shaded area defines the approximate limit of winterkill lakes that are likely to be suitable for trout farming.

rainbow trout on a seasonal basis on the Canadian prairies and the potential for growth and development of this industry is excellent.

Description of Study Area

The experimental lakes are located in southwestern Manitoba (approximately 50°30′N, 100° 10′W) in the Erickson–Elphinstone district, immediately south of Riding Mountain National Park (Fig. 1). It lies within the Minnedosa pothole area which is famous for duck production.

The study area lies at an elevation of 540–610 m (1800–2000 ft) on a prominent range of hills underlain by shales of the Cretaceous period. Surface deposits are glacial drift, predominantly shale and limestone, that occur as terminal and end moraines. The topography is gently undulating to rolling (Fedoruk 1971). The prevalent soil is a thin layer of grey-wooded forest soil, although black and organic soils occur. Most of the land is cultivated, but stands of natural forest (mainly *Populus tremuloides* Michx) remain on hillsides, low areas, and lake shores (Weir 1960).

Lakes in the study area are numerous, occurring as kettles or sumps within and between the moraines. The incidence of lakes greater than 1 ha is approximately four per km^2 (10 lakes/square mile) (Fedoruk 1971). Some 65% are 1–2 ha in area, 32% are 2–8 ha, and 3% exceed 8 ha. The largest is about 1000 ha. The lakes are relatively shallow, less than 1% exceeding 4 m maximum depth. Most are landlocked and receive only ground seepage or intermittent runoff from small cultivated watersheds. Some have outflow in high water years and a few are located on annually flowing systems.

Winterkill occurs regularly, except in some of the larger (usually over 40 ha) or deeper (usually over 8 m) lakes (Johnson et al. 1970). Few contain large native fishes, but the fathead minnow (*Pimephales promelas*) and the brook stickleback (*Culaea inconstans*) are permanent residents of perhaps 10–20% of the lakes even where dissolved oxygen falls below 2 mg/liter in late winter.

Some chemical features of lakes stocked with rainbow trout in 1972 are summarized in Table 1.

The salinity of about two-thirds of the experimental lakes ranges from 1000 to 3000 µhmo/cm. Those with salinities exceeding 800 µmho/cm are predominantly magnesium sulphate lakes. Less saline lakes are usually calcium and magnesium bicarbonate types. The lakes are well buffered and changes in pH on a seasonal or diurnal basis are slight. The range of nutrient concentrations is exceptionally wide.

Most lakes of the study area are highly productive. *Gammarus lacustris* (Amphipoda), the dominant trout food, is abundant as are corixids and chaoborids. Zooplankton densities recorded from some of the larger lakes in August 1970 ranged from 185 to 457 individuals per liter (Sunde et al. 1970). Phytoplankton production is exceptionally high. Dense *Aphanizomenon flos-aquae* blooms are prevalent in many of the lakes from mid-July to late August, often attaining levels of 0.5–2.0 ml/liter and reducing Secchi depths from over 2.5 m to 0.2 or 0.3 m. Summerkill may occur on some of the *Aphanizomenon* lakes, as a result of precipitous collapse of the algal bloom followed by rapid bacterial decomposition of the dead cells. This decomposition reduces dissolved oxygen, usually supersaturated prior to collapse of the bloom,

Table 1. Concentration ranges of some chemical constituents of experimental lakes in the Erickson–Elphinstone district in 1972 (rounded values). (Specific conductance = 400–6500 µmho/cm at 25 C; pH = 7.9–9.4; dissolved O_2 = 0–26 mg/liter.)

Major ions	(*mg/liter*)	Nutrients	(µg/liter)
Ca	63–160	NH_4–N	0–2500
Mg	38–1100	NO_3–N	0–400
Na	3–615	DON	0–10,000
K	11–120	PO_4–P	0–200(870[a])
Cl	1–170	DOP	0–200(2200[a])
SO_4	17–5300	DOC	100–4000
HCO_3	100–600	Chlorophyll *a*	10–1150

[a] Data from Lake 103, which receives sewage lagoon effluent.

almost to zero throughout the water column for several days following the collapse (Barica 1973).

Methods

Lakes of varying area, depth, and salinity were selected for experiments to evaluate limiting effects of various physical and chemical variables on trout production.

Water temperature and dissolved oxygen have been monitored on a regular basis in the summer since 1970, and dissolved oxygen has been measured irregularly in the winter since 1969. Selected chemical features of these lakes were measured irregularly in the summer and winter of 1969 and 1970 and intensively in the summers of 1971–73. Morphometric surveys have been completed on most of the key experimental lakes.

A variety of strains of rainbow trout have been used for stocking the lakes. They include at least one domestic, fall-spawning stock from each of the states of Montana, Idaho, and Washington and two wild, spring-spawning stocks from British Columbia. Growth and survival of a number of strains are being tested and brood stocks are being retained for a selective breeding program.

Two basic size-groups of trout have been planted: 2–3 cm advanced fry and 5–8 cm fingerlings. The smaller trout, planted in 1968, 1969, and 1970, were imported from the United States as eyed eggs and reared in the Manitoba Government trout hatchery at West Hawk Lake. Most of the larger trout planted in 1969, 1970, and 1971 were imported from the United States as fingerlings and planted directly into experimental lakes. In 1972, they were received from Idaho and British Columbia as eyed eggs and were reared at the Freshwater Institute experimental hatchery at Balmoral, Manitoba. Planting statistics are summarized in Table 2.

Fingerling trout were planted as soon as possible after spring break-up. In 1970, 1971, and 1972, 100 or more were caged in each lake to provide a measure of stocking mortality. The harvest usually commenced the 2nd wk of October, about 3 wk before freeze-up. Most of the trout were recovered during the open water fishery, but the harvest was completed as a winter fishery that lasted as late as mid-December. A great majority of the trout were recovered in gill-nets, but trap- and poundnets, beach and Scottish pair seines and trawls have been used experimentally to improve the quality of trout landed.

Results

Trials with rainbow trout advanced fry have been unsuccessful. Rates of recovery and production have been low, never exceeding 17.2% and 21.0 kg/ha, respectively, and few of the trout attained a minimum marketable size of 200 g round weight in one summer (Sunde et al. 1970).

Results obtained in experimental plantings of 5–8 cm fingerling rainbow trout have been very

TABLE 2. Planting and harvest summary for experimental lakes stocked with 5–8 cm rainbow trout (*Salmo gairdneri*) fingerlings from 1969 to 1972.

		1969	1970	1971	1972
			Lakes		
Number		3	17	20	17
Max depth (*m*)	Range	3–8	1–5	1–5	1–5
Area (*ha*)	Range	8–25	1–10	1–15	1–23
	Mean	14.4	5.7	6.6	7.1
			Planting		
Date 2/3 complete		May 15	May 26	May 6	May 10
Mean weight of fish (*g*)[a]		3.8	3.9	3.2	2.9
Total number		39,500	65,830	100,480	169,700
Rate (trout/ha)	Range	62–1354	62–2120	62–2372	494–6178
	Mean[a]	912	680	766	1406
			Recoveries		
Percent	Range	9–70	0–86	0–74	0–58
	Mean[a]	17.4	32.7	41.3	27.7
Final size (*g*)	Range[b]	266–383	153–241	176–391	116–397
	Mean[a]	335	204	252	207
Production (*kg/ha*)	Range	12–132	0–115	0–249	0–313
	Mean[a]	53.0	45.6	79.8	80.3

[a] Weighted means — statistics from all lakes are combined as in one large lake.
[b] Range of means from individual lakes.

promising. Growth, survival, and yield have been highly variable, but prospects for establishment of a successful trout farming industry on prairie winterkill lakes are excellent.

A summary of recoveries from experimental lakes stocked with 5–8 cm fingerlings from 1969–72 appears in Table 2.

Growth

Growth of rainbow trout in prairie winterkill lakes is highly variable and appears to depend on a number of factors, including initial size of stock, stocking rates (and yields), length of growing season, variability between strains, and lake morphometry and fertility.

The final size attained by trout at the time of harvest is directly proportional to initial size of fingerlings planted, but the relation between final and initial size is poor because of the interaction of other factors. However, fingerlings of 5–8 cm fork length (2–5 g) normally produce trout of marketable size in the 6-mo period of open water that prevails in this area.

Stocking rates have little apparent effect on the final size of trout at planting rates below 2500 fish/ha, even in lakes that had been stocked quite heavily for 1 or 2 yr previously. However, at planting rates greater than 4500 fish per hectare, drastic reductions in final size were observed. In 1972, the final mean size of trout planted at rates under 2500 fish/ha and over 4500 fish/ha were 266 g and 130 g, respectively.

The length of time the trout exist in the experimental lakes must obviously determine their final size, but the relation between planting date and final size is poor because of the interaction of other important factors. The small size attained by trout in 1970 is attributed mainly to late planting dates.

Various strains of trout exhibit differing potential for growth. Growth performance of wild strains of rainbow trout in experimental lakes has almost always been poor and Ayles (1973) showed that domestic strains grew significantly faster than a wild strain in 1972.

Survival

Survival of rainbow trout in winterkill lakes is also highly variable (Table 3). This is attributed almost exclusively to summerkill which is prevalent on many of the winterkill lakes of the study area. It occurs with varying degrees of severity so fish kills may be partial or total. This is confirmed by observation of fish kills on lakes containing two basins. Dissolved oxygen may fall to critical levels in one basin whereas the other retains tolerable levels.

TABLE 3. Frequency of percent recoveries of rainbow trout from experimental lakes stocked with 5–8 cm rainbow trout fingerlings from 1969 to 1972.

% recovery	1969	1970	1971	1972
0	–	3	1	3
1–9	1	1	4	4
10–19	–	2	1	2
20–29	–	2	2	2
30–39	–	2	3	2
40–49	–	2	4	3
50–59	–	1	2	1
60+	2	4	3	–
Mean	17	33	41	28

Variability in survival of rainbow trout is attributed mainly to summerkill because of the absence of other plausible explanations:

1, All kills observed have been associated with critically low conditions of dissolved oxygen and there has never been any obvious sign of disease or infection in fish killed.
2, Planting mortality, assessed by use of caged samples of trout since 1970, has always been low. Overall survival for the first 2–16 days (usually 7–10 days) generally exceeds 98% and is seldom lower than 90%.
3, Predation has been discounted as a serious problem because the waters of the experimental lakes are not clear enough for efficient hunting by loons, mergansers, and mink. The trout are sometimes vulnerable to gulls and terns for the first few hours after stocking, however, and wading birds such as herons and bitterns probably take a few trout in the spring and early summer.
4, Harvest efficiency with gillnets is high, and as most lakes are fished until catches fall below three trout per 50 m net night, it is estimated that less than 5% of the trout available escape the fishery.

Survival is not correlated with stocking rates below 2500 fish/ha, but at rates above 4500/ha survival appears to be significantly lower. This, however, has not yet been substantiated and appears to be an artifact of partial summerkill.

Ayles (1973) found that survival was higher in domestic than in wild strains of rainbow trout.

Yield

Production (kg/ha) is also highly variable because of the high incidence of summerkill, which in most cases is only partial. Yield does, however, increase with stocking rates to at least 2500 trout/ha and possibly to 4000/ha. At higher stocking rates, yields diminish and the trout no longer attain marketable size. The highest yield yet attained is 313 kg/ha in a lake that had been planted for three consecutive years at annually increasing planting rates (1500, 2000, and 4500 fish/ha). Yields in the first 2 yr were 70 and 250 kg/ha.

Several heavily stocked lakes have yielded more than 150 kg/ha for 1 or 2 yr with no obvious decline in size of fish produced or in abundance of their main food organism, *Gammarus lacustris* (Amphipoda). High planting rates are being maintained in several lakes to determine their long-term productive capacity and the effect of continuous exploitation on abundance and availability of *Gammarus*.

QUALITY

The color of the flesh of rainbow trout raised in most winterkill lakes is highly attractive. The main food organism available to the trout is *Gammarus* and a steady diet of this crustacean imparts a deep pink color to the flesh. Some lakes containing large populations of native minnows or sticklebacks may produce trout with flesh that is light in color, but as such lakes are relatively few in number it poses a minor problem, and such lakes are readily identified and avoided.

The flavor of the trout is exceptionally good in most lakes, but may be highly unsatisfactory in others because of muddy flavor. Muddy flavor describes an earthy or musty off-flavor that may occur in trout and other fishes from a wide variety of freshwater lakes and streams. It is present in 15–20% of the Erickson experimental lakes and may be more prevalent in other areas. As affected fish are almost valueless for commercial sale, the muddy flavor problem poses a serious risk to trout farming.

Muddy flavor has been under investigation for several years. The causative substances, geosmin and perhaps 2-methylisoborneol, and the carrier organisms, algae such as *Oscillatoria* and *Lyngbya* sp., have been identified (M. Yurkowski personal communication). No practical method for prevention of the muddy flavor has been found, but it has been effectively masked by a smoking and canning process that produces a highly acceptable product (Iredale 1973).

Current investigations include tests of the consistency of muddy flavor of trout within lakes, and live trout have been transferred to "clean" water to test the rate of loss of muddy flavor. Samples from these experiments have not yet been subjected to taste panel tests.

Muddy flavor lakes are presently detectable only by trial plantings of rainbow trout. This method is not impractical because the presence or absence of muddy flavor in lakes is highly consistent, and light plantings of trout are sufficient for a test. New methods for detection of "muddy" lakes are under investigation. The distribution of algae and macrophytes and variations in water chemistry in muddy and clean winterkill lakes are being compared in the hope that muddy lakes may be identified (and avoided) by means of indicator organisms or predictive indices based on water chemistry.

The quality of the trout also suffers somewhat because of current harvest methods. A number of different types of fishing gear have been tested and gillnets have proved the most efficient and economical. Unfortunately, however, they can't be used effectively until late fall, when water temperatures are below 8–10 C, and even then the spoilage and damage to trout is high if the nets are not lifted at short intervals (preferably twice per day) and the trout carefully removed from the nets. A high proportion of the trout also have net marks that greatly detract from their appearance. The quality of trout caught in trapnets and beach and pair seines is excellent, but catch success has been variable. Tests are to continue with trapnets and seines of modified design, and recent advances in the technology of electrofishing make this a highly attractive method worthy of future consideration.

Status of the Industry and Priorities for Future Research

The feasibility tests of 1968 and 1969 aroused intense public interest in trout farming and in 1970 the private sector became involved. Expansion of the industry was rapid and by 1972 almost 1500 individuals in Manitoba, Saskatchewan, and Alberta took out licenses or permits to stock trout. Some 1.8 million rainbow trout fingerlings were planted in 1700–1800 natural lakes and farm dugouts. Estimated production from Manitoba and Saskatchewan was 215,000 pounds, valued to the producer at $200,000.

Many basic techniques necessary for management of a trout farming industry in prairie winterkill lakes have already been established. They include planting and harvest dates and methods, size of stock, planting rates, morphological and chemical limitations, and predation and competition effects. Experimental plantings are continuing for the purpose of improving management techniques and evaluating the long-term productive capacity of winterkill lakes for trout. A fish genetics program has also been initiated to develop superior strains of rainbow trout for prairie winterkill lakes. The growth and survival of three domestic and two wild strains have already been tested by matched plantings in winterkill lakes, and the largest individuals of the strains that performed best, plus randomly selected stock, have been retained as brood stock for a selective breeding program.

Three serious problems impede development of trout farming in winterkill lakes. Muddy flavor and harvest efficiency have already been discussed, and the third problem, summerkill, has been mentioned. Summerkill occurs when nearly pure cultures of *Aphanizomenon flos-aquae* attain high bloom concentrations and then die off suddenly, creating temporary anoxic conditions as a result of bacterial decomposition of the dead algal cells (Barica 1973, 1974). It is by far the most serious problem yet encountered. At least 80% of poor recoveries from experimental lakes are attributable to partial or total summerkill (see Table 3) and it is the high risk associated with summerkill that deters a more rapid expansion of the industry.

An alleviation of the summerkill problem has the highest priority in current investigations related to trout farming in winterkill lakes. The chemical variables associated with summerkill lakes and the physical, chemical, and biological processes accompanying summerkill are under intensive investigation. This is the preliminary step in studies designed to provide methods for summerkill prediction and prevention.

Summerkill prediction — Risks presently associated with trout farming could be greatly reduced if practical methods were available for identification of problem lakes or the prediction of summerkill. Winterkill lakes are so numerous on the prairies that a large trout farming industry would exist if success could be guaranteed on as few as 20% of the lakes available. With this in mind, the water chemistry of a number of high- and low-risk lakes (previously classified by trout plantings) is being compared, and attempts are being made to formulate predictive indices for the identification of high-risk summerkill lakes. In addition, macrophyte and algal distribution of high- and low-risk lakes will be compared and indicator species for the identification of summerkill lakes will be sought. The possible application of remote sensing by aircraft and satellite to identification of problem lakes will also be investigated.

Summerkill prevention — Most high-risk summerkill lakes are highly productive and have great potential for trout farming, so practical methods of summerkill prevention would be the most direct and useful solution to this serious problem. Summerkill could be greatly reduced or prevented if methods were available to depress algal blooms or prevent their sudden collapse.

The precipitous collapse of *Aphanizomenon* blooms is probably caused by exhaustion from the water of some element (presumably nutrients) vital to their physiology. Tests have shown that phosphorus availability in the lake declines greatly just prior to the collapse. Tube experiments in a high-risk summerkill lake will be conducted in 1974 to see if phosphorus spiking of the water might be effectively used to prevent or significantly prolong the *Aphanizomenon* collapse and thereby avert summerkill.

Several methods for prevention of summerkill by suppression of *Aphanizomenon* blooms are being tested. A lake aeration system, using compressed air distributed through perforated hoses,

TABLE 4. First summer growth of walleye, whitefish, and whitefish × cisco hybrids in prairie winterkill lakes (mean round weight in grams and mean fork length in centimeters).

Date	Lake	Walleye		Whitefish		Whitefish × cisco hybrids	
		Weight	Length	Weight	Length	Weight	Length
Oct. 1, 1970	522	46	15.8	–	–	–	–
Dec. 14, 1971	522	136	23.9	–	–	–	–
Sept. 20, 1972	522	–	12	–	–	–	–
Oct. 20, 1971	302	58	15.6	409[a]	28.6[a]	–	–
Oct. 28, 1971	971	–	–	71	17.5	–	–
Nov. 5, 1970	391	–	–	73	17.0	–	–
Nov. 18, 1971	391	–	–	66	16.9	–	–
Oct. 4, 1972	391	–	–	35	14.2	50	15.6

[a] Several hundred whitefish from Lake 391 were overwintered in Lake 302 (by means of an aeration system) in an experiment designed to measure second summer growth in a winterkill lake.

has been tested and will be operated throughout the summer of 1974 on a high-risk summerkill lake. *Aphanizomenon* blooms most readily when the lake surface is warm and undisturbed. The aeration system is designed to inhibit growth and reproduction of this algae by circulating the upper half of the lake. Small areas of the lake that are intensively aerated may also create an oxygen-high refuge for the trout in case of a severe kill.

An algicide was tested in 1973 on a 1 ha lake that had partially summerkilled in 1971 and 1972. It was treated on July 11 with 45.4 kg (100 lb) of copper sulphate (to achieve a concentration of 1 mg/liter copper). At the time of treatment, this lake was dominated by blue-green algae and an *Aphanizomenon* bloom was developing. Within 2 days of treatment, the lake was dominated by green algae and diatoms which persisted until freeze-up. No oxygen depletion was recorded and 74% of the rainbow trout stocked were recovered in October; recoveries of trout from this lake in 1971 and 1972 had been only 8% and 13%. This method will be retested on several high-risk summerkill lakes in 1974.

Tube experiments are also proposed to test the practicability of two other chemical methods of *Aphanizomenon* suppression — pH reduction and phosphorus precipitation.

Culture of Other Fishes in Winterkill Lakes

Feasibility tests of fish culture in prairie winterkill lakes have included other species besides rainbow trout. Kokanee salmon (*Oncorhynchus nerka kennerlyi*) have been tested twice in experimental lakes, but success was poor because of slow growth. In one lake the mean size attained in one summer was only 41 g, in the other the final mean size was only 60 g. The largest individual was 130 g, which is far short of the minimum marketable size of about 200 g. The kokanee in one of these lakes survived two winters. Their size after the second summer of growth averaged 244 g and in the third summer was 314 g. Rainbow trout that survived one winter in an experimental lake averaged 1062 g after two summers of growth. The largest was 2040 g. The lakes planted with kokanee were only briefly sampled, so no measure of recovery rate is available. Catches, however, were fair and the rate of recovery should have exceeded 10–20%.

Small plantings of several Pacific salmon species (*Oncorhynchus* spp.), brook trout (*Salvelinus fontinalis*), and possibly Arctic char (*Salvelinus alpinus*), are planned for the future to test growth performance and survival in winterkill lakes.

Use of winterkill lakes as nursery ponds for production of advanced fingerlings of lake whitefish (*Coregonus clupeaformis*), walleye (*Stizostedion vitreum vitreum*), and lake whitefish × cisco hybrids (*C. clupeaformis* × *Coregonus* spp.) has also been tested. Large fingerlings are of value for restocking of sport and commercial waters in resource-enhancement programs.

Growth has been excellent, despite the fact that swim-up fry (1 cm long) were not available for planting until about a month after spring break-up. The size attained by these species in one summer is summarized in Table 4. The great variation in growth of walleye appears to be related to the seasonal abundance (= competition?) of native minnows present in the lakes planted.

Rate of survival of whitefish and walleye has not yet been measured. The numbers planted in the spring have been only estimates and the fall fishery has consisted only of brief sampling catches.

In 1972, 2500 walleye advanced fingerlings were marked by finclipping and transplanted to an experimental lake containing native and introduced stocks of walleye, to test the comparative value of stocking programs using swim-up fry and advanced fingerlings. Recoveries of the advanced fingerling stock to date have been extremely poor, but further transplants of walleye and whitefish advanced fingerlings are planned.

Experimental plantings of walleye and whitefish in prairie winterkill lakes will be continued to provide fingerlings for the experiments described above and to allow further studies of the following: survival rates; planting rates and their relation to final fingerling size and yield; development of effective methods for live capture of advanced fingerlings; determination of the effect of competition by native minnows and sticklebacks.

Acknowledgments

We gratefully acknowledge the assistance and cooperation of several scientists and technicians of the Freshwater Institute and the Rockwood experimental trout hatchery who have participated in this project. We also thank the many landowners who granted permission for our use of their lakes for these experiments.

AYLES, G. B. 1973. Comparative growth and survival of matched plantings of wild and domestic rainbow trout in prairie potholes. Fish. Res. Board Can. Tech. Rep. 382: 13 p.

BARICA, J. 1973. Changes in water chemistry accompanying summer fish kills in shallow eutrophic lakes of southwest Manitoba. Proc. Symp. on Lakes of Western Canada. Univ. Alberta, Water Res. Cent. Publ. No. 2: 228–241.

1974. Some observations on internal recycling, regeneration and oscillation of dissolved nitrogen and phosphorus in shallow self-contained lakes. Arch. Hydrobiol. (In press)

FEDORUK, A. N. 1971. Water and fish capability. South side Riding Mountain National Park A.R. D.A. area No. 7038. Man. Dep. Mines Nat. Resour., Can. Land Inventory Proj. Rep. No. 8: 121 p.

IREDALE, D. G., AND K. J. SHAYKEWICH. 1973. Masking or neutralizing muddy flavor in rainbow trout (*Salmo gairdneri*) by smoking and canning processes. J. Fish. Res. Board Can. 30: 1235–1239.

JOHNSON, L., G. H. LAWLER, AND L. A. SUNDE. 1970. Rainbow trout farming in central Canada. Fish. Res. Board Can. Tech. Rep. 165: 17 p.

SUNDE, L. A., J. WHITAKER, AND G. H. LAWLER. 1970. Rainbow trout production in winterkill lakes, p. 57–65. *In* E. Schneberger [ed.] A Symposium on the Management of Midwestern Winterkill Lakes. Publ. North Cent. Div. Am. Fish. Soc. 75 p.

WEIR, T. R. [ed.] 1960. Economic atlas of Manitoba. Manitoba Dep. Ind. Commer. 81 p.

Experimental Lakes Area: Whole-Lake Experiments in Eutrophication[1]

D. W. SCHINDLER AND E. J. FEE

Department of the Environment
Fisheries and Marine Service, Freshwater Institute, Winnipeg, Man. R3T 2N6

SCHINDLER, D. W., AND E. J. FEE. 1974. Experimental Lakes area: whole-lake experiments in eutrophication. J. Fish. Res. Board Can. 31: 937–953.

The following whole-lake experiments are described:

Lake 227, fertilized for 5 yr with phosphate and nitrate, has shown an enormous increase in phytoplankton, in spite of low carbon concentrations. The carbon necessary for production of algal blooms was found to invade from the atmosphere.

Lake 304, eutrophied by fertilization with phosphorus, nitrogen, and carbon in 1971 and 1972, recovered rapidly when phosphorus fertilization was terminated.

Lake 226 was split in half with a curtain. One half was fertilized with carbon and nitrogen and the other was fertilized with phosphorus, carbon, and nitrogen. The half of the lake receiving phosphorus developed an algal bloom and the other half did not.

Lake 302, which had carbon, nitrogen, and phosphorus added to the hypolimnion, did not develop algal blooms in summer. Small phytoplankton blooms were found under ice in early December, but all nutrients were efficiently sedimented and unavailable the following year.

The above studies illustrate clearly that phosphorus control is an efficient primary step in preventing or checking eutrophication problems.

A review of other published and ongoing studies in the Experimental Lakes Area is given, illustrating the role which large-scale experiments can play in interpreting environmental problems.

SCHINDLER, D. W., AND E. J. FEE. 1974. Experimental Lakes area; whole-lake experiments in eutrophication. J. Fish. Res. Board Can. 31: 937–953.

Nous décrivons les expériences suivantes sur des lacs entiers:

Le lac 227, fertilisé au phosphate et au nitrate pendant 5 ans, montre une énorme augmentation de phytoplancton, en dépit de faibles concentrations de carbone. On s'est rendu compte que le carbone nécessaire à la production des poussées algales provenait d'une invasion atmosphérique.

Le lac 304, eutrophié par fertilisation au phosphore, à l'azote et au carbone en 1971 et 1972, s'est rapidement rétabli lorsque la fertilisation au phosphore a cessé.

On a divisé le lac 226 en deux à l'aide d'un rideau. Une moitié a été fertilisée au carbone et à l'azote, l'autre au phosphore, au carbone et à l'azote. La moitié du lac qui avait reçu du phosphore a subi une poussée algale, et l'autre n'a pas eu de poussée.

Le lac 302, dans lequel on avait ajouté du carbone, de l'azote et du phosphore dans l'hypolimnion, n'a pas eu de poussées algales en été. De courtes poussées phytoplanctoniques ont été observées sous la glace au début de décembre, mais toutes les substances nutritives se sont efficacement sédimentées et n'ont pas été disponibles l'année suivante.

Ces études démontrent clairement que le contrôle du phosphore est une première étape efficace pour la prévention ou l'arrêt des problèmes d'eutrophisation.

Nous passons en revue d'autres études publiées ou en voie de publication sur la région des lacs expérimentaux, mettant en relief le rôle que peuvent jouer des expériences à grande échelle dans l'interprétation des problèmes de l'environnement.

Accepted December 31, 1973

---

[1] This paper, part of a special issue that comprises a comprehensive review of Limnology in Canada, was prepared to mark the 19th Congress of the International Association of Limnology (SIL), in Winnipeg, Man., during August 1974.

Printed in Canada (J3258)

LAKE eutrophication is a major environmental concern of our society at the present time. The essence of the eutrophication problem is to determine the effect of culturally elevated amounts of phosphorus and nitrogen on algal standing crops in lakes, and to develop suitable management techniques for eutrophication control.

Several types of approaches to the relationship between algal standing crops and nutrients have been made, the most familiar being to observe the responses of the algal standing crop to different nutrient concentrations or nutrient inputs. This approach is expensive, as many culturally enriched lakes have diffuse nutrient inputs. Good nutrient budgets are nearly impossible to obtain. Furthermore, there are usually no data for the transition period between the lake in its natural condition and in its fully eutrophic state because there is no compulsion to study a lake until it has serious problems. Toxic substances as well as nutrients usually enter such lakes, so that complicating synergistic effects must also be studied.

Other approaches to eutrophication-related problems have been made in the laboratory, using nutrient-uptake studies by bottled or cultured algae, studies of nutrient–sediment interactions, etc. to develop mathematical models of the eutrophication process. Such approaches, if applied to a whole ecosystem, assume that when a natural system is perturbed it will respond in a manner predictable on the basis of the physiologies of the organisms present before perturbation. Because the biological components of a perturbed system invariably change, such assumptions are questionable, and conclusions about eutrophication based on laboratory studies of a few (usually easily cultured and nonrepresentative) test organisms must be viewed with suspicion.

A more realistic eutrophication study is a whole-lake experiment in which budgets of all major nutrients are accurately manipulated. By changing the nutrient budgets in a precisely known way, one can observe the actual response of a whole, natural system to known enrichments with different rates of a single nutrient or different combinations of nutrients. The results give a clear answer about the environmental importance of the nutrient. Realizing this, in 1966 the Canadian government authorized the establishment of an Experimental Lakes Area in northwestern Ontario, and the Freshwater Institute was commissioned with the task of studying interactions between nutrients and lake eutrophication (Fig. 1).

As Johnson and Vallentyne (1971) pointed out, whole-lake experiments are not new. At the time the Experimental Lakes Area was established, much information had been gathered on the response of fish yields to single bulk additions of fertilizers to water bodies. However, no experiments had been specifically designed for elucidating the causal connection between nutrient loading and eutrophication. In particular, nothing was known of the range of nutrient loading rates likely to be of practical concern in causing lake eutrophication; previous additions were usually much higher than rates known to cause serious eutrophication problems. Further, the unnaturalness of a single bulk nutrient addition makes many of the observed consequences of questionable generality as most eutrophied lakes receive a more or less continuous nutrient load, at least during the ice-free season.

As the present program was established with the problem of lake eutrophication specifically in mind, certain complicating factors of previous experiments could be eliminated. First, we had access to a large number of small lakes with similar morphometry, chemistry, and phytoplankton populations. The lakes had no large populations of macrophytes to obscure the relations between the nutrients and algae, that we desired to study. Second, we had complete control over several lakes and watersheds, and could perform experiments that would be impractical in a more populated area. Third, the hydrology and geology of the region was very convenient for our purpose because it is a headwater area and thus no nutrients enter an experimental lake from upstream lakes. Also, our lakes lie in basins sealed by bedrock so that inflows and outflows of nutrients from groundwater are negligible. Bedrock and overburden in the area are chemically simple and sparingly soluble. These factors greatly simplify the basic problem of measuring the low natural rates of nutrient input.

WHOLE-LAKE EXPERIMENTS

An ideal problem for a whole-lake experiment became apparent just at the time the Experimental Lake Area had been established. This was the controversy over whether the eutrophication of lakes could be prevented by insufficient carbon supplies. A number of investigators (Lange 1967, 1970; Kuentzel 1969; Kerr et al. 1970) performed calculations on observational data and laboratory experiments which they believed provided proof that eutrophication was directly linked with available carbon. On the basis of these arguments, industrialists criticized the International Joint Commission of the St. Lawrence Great Lakes for their proposed controls on phosphorus in the Lake Erie and Lake Ontario basins (Anon. 1970).

Engineers, confused by the limnological arguments, began to advocate total nutrient removal from the more serious nutrient sources instead of phosphorus control, undoubtedly a costly procedure which would require considerable time for the development of technology, let alone construction of suitable removal facilities.

In the initial surveys done at ELA, we found that the lakes contained less dissolved inorganic carbon (DIC) than those of any lake area described in the literature — due, no doubt, to the nearly total absence of calcareous material in bedrock or glacial overburden and low weathering rates in the drainage area. We decided to add phosphorus and nitrogen to one of these lakes, 227, to see how far eutrophication could develop under low-carbon conditions. Amounts added were 0.48 g of P and 6.29 g of N/m^2 annually.

Results of this experiment were striking. An algal bloom developed within a few weeks after fertilization began, in response to phosphorus and nitrogen inputs of about 10 times natural levels (Schindler et al. 1971, 1973b). Whereas natural lakes in the area usually have 2–5 μg/liter of chlorophyll in the euphotic zone in midsummer, lake 227 developed blooms of up to 200 μg/liter (Fig. 2). The chrysophycean and cryptophycean flora typical for natural lakes in the area was replaced by cyanophytes and chlorophytes, chiefly *Oscillatoria*, *Lyngbya*, *Pseudoanabaena*, *Oocystis*, and *Dictyosphaerium* (Kling and Holmgren 1972). Thus, in spite of extremely low DIC concentrations (as low as 20 μmoles/liter in the epilimnions of small unfertilized natural lakes in midsummer), highly eutrophic conditions were produced by phosphorus and nitrogen additions alone. Since DIC is much higher in all lakes of economic importance, carbon control does not merit serious consideration as a management strategy. Further information is given by Schindler et al. 1971, 1973b.

The lake 227 fertilization suggested several other experiments, utilizing whole lakes or large parts thereof. At midday during summer the DIC concentration in the epilimnion of lake 227 was

FIG. 1. An aerial photo of the center of the Experimental Lakes Area, showing lakes, including those used in fertilization experiments and location of the main laboratory. Morphometry and more detailed descriptive information are given by Brunskill and Schindler (1971) and other papers in J. Fish. Res. Board Can. 28(2).

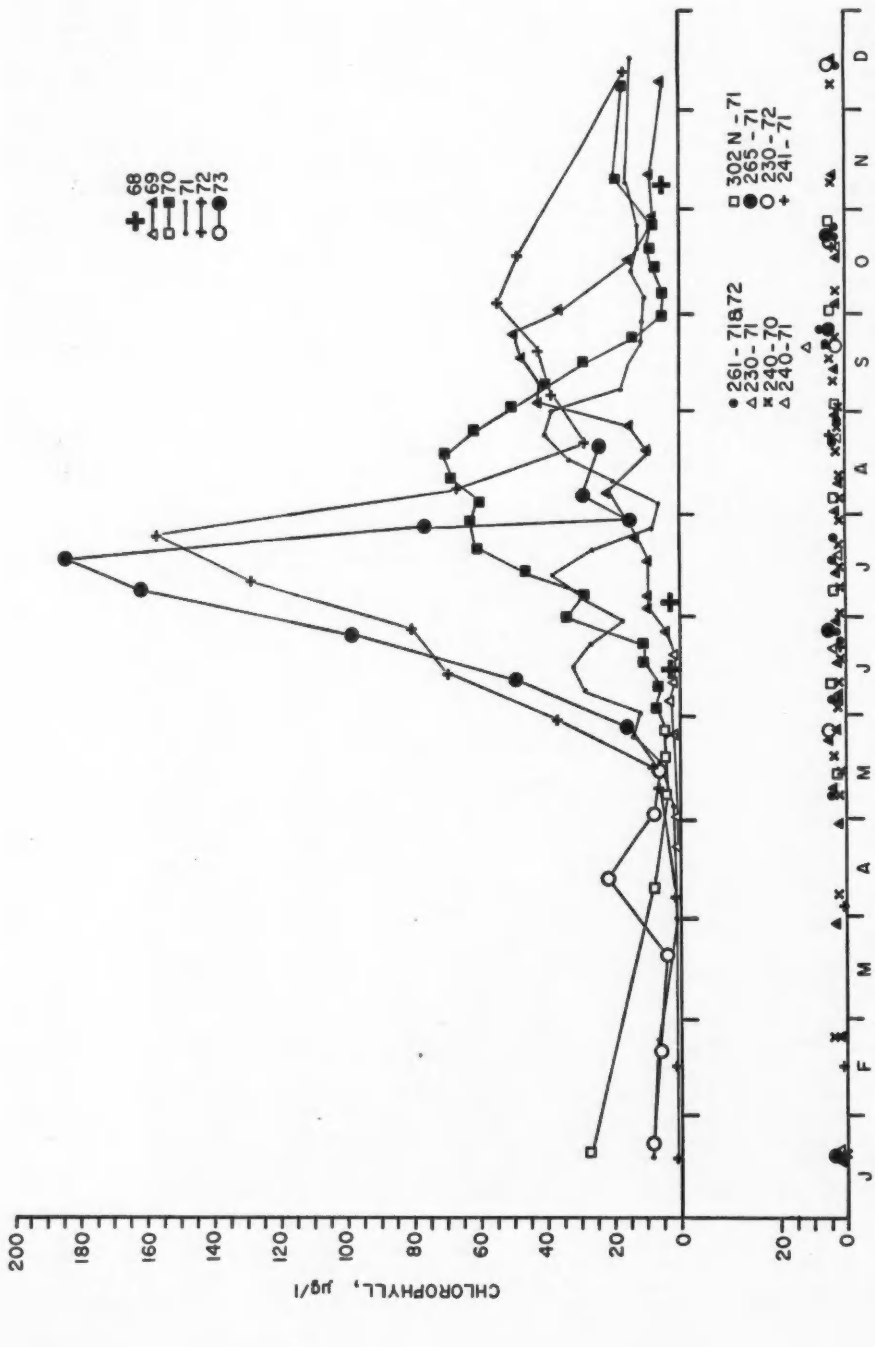


FIG. 2. A comparison of phytoplankton standing crops (as chlorophyll *a*) in the epilimnions of natural unfertilized lakes (*lower panel*) and lake 227, fertilized with 0.48 g of P and 6.29 g of N/m² annually (*upper panel*). All lakes are under 13 m deep. Note that lake 227 had a standing crop similar to other lakes prior to fertilization. Large inputs of P and N will thus cause severe eutrophication problems regardless of how low carbon concentrations are. The necessary carbon is drawn from the atmosphere.

drawn as low as 1–5 μmoles/liter by high rates of photosynthesis. Such concentrations were insufficient to support photosynthesis for much of the day (Schindler and Fee 1973a, b). Invasion of CO^2 from the atmosphere allowed the lake to correct its carbon deficit to a large degree (Schindler et al. 1973b). Up to 95% of the annual input of carbon to the lake was supplied by the atmosphere, and phytoplankton standing crops were so high (200–600 mg chlorophyll/m^2) that they were probably light limited (Talling et al. 1973). Experiments dealing with gas exchange and associated CO_2 uptake by algae are described by Schindler et al. 1972, 1973a, c; Schindler and Fee 1973b; and Emerson et al. 1973.

Another interesting result of the lake 227 experiment was that mass-balance calculations indicated that there was little return of phosphorus from sediments, either during summer stratification or during winter (Schindler et al. 1973b), even though the lake was anoxic below 5 m in both seasons. This result was also directly demonstrated with radioactive techniques (Lean and Schindler unpublished data). Further radioisotope experiments revealed that phosphate added either to epilimnion or hypolimnion was rapidly removed by microplankton[2] of 0.45–10 μ in diameter. On the basis of these results, we hypothesized that if nutrient-rich influents were directed into the hypolimnion rather than the epilimnion, at a depth below the euphotic zone, uptake by microplankton and subsequent sedimentation would allow the nutrient to be removed from the lake without producing noxious algal blooms.

To test this hypothesis, we chose lake 302 (Brunskill and Schindler 1971) which had two basins, one 10 and the other 13 m deep, separated by a narrows where water was less than 2 m deep (Fig. 1). One basin was held as a control, and the other had nutrients (phosphoric acid, ammonium chloride, and sucrose) pumped into the hypolimnion at a depth of 8 m, well below the thermocline. Rates of addition were 0.54 g P, 2.79 g N, and 3.73 g C/m^2 of lake surface per year, added over a 21-wk period between mid-May and mid-October.

As we expected, no evidence of a summer algal bloom, or of change in species composition, could be detected in the epilimnion of the fertilized basin. An increase was observed in late fall phytoplankton, but it was small compared to the response of lakes to epilimnetic fertilizer additions in summer (Fig. 3). Added fertilizer was rapidly taken up by hypolimnetic suspended matter and sedimented. As of January 1973, 90% of the phosphorus, 70% of the nitrogen, and 100% of the carbon added as fertilizer during 1972 had disappeared (Fig. 4).[3] The removal mechanism appeared to be identical to that in lake 227, since aonxic conditions prevailed through much of the summer. An enormous increase in small (0.45–10 μ) microplankton (measured as ATP) occurred at the depth of the nutrient inflow (Rudd and Hamilton 1973). Thus, contrary to the widespread belife that oxygen depletion must allow phosphorus to be liberated from sediments, the sediments of Canadian Shield lakes appear to be efficient phosphorus sinks, whether oxygen is present or not. It is possible that small resorts or cottage developments, operating seasonally on lakes with well-developed hypolimnions which contain no important sport or commercial fishes, might effectively dispose of their wastes by directing outflows from septic-tanks or sewage treatment plants to the hypolimnion, rather than allowing them to seep into surface waters. Further investigation is, of course, required before such a novel procedure could be endorsed for widespread use.

As mentioned above, although the standing crop of phytoplankton in lake 227 increased enormously after fertilization, phytoplankton in the lake did show symptoms of carbon shortages at midday when standing crops reached 100 μg/liter as chlorophyll *a* (Schindler and Fee 1973a, b). To test the possibility that carbon additions of the magnitude expected with sewage inflows would allow still higher standing crops of algae, we began an experiment in lake no. 304 (Fig. 1), adding H_3PO_4, NH_4Cl, and sucrose in sufficient quantities to constitute an annual input of 0.40 g of P, 5.2 g of N, and 5.5 g of C/m^2.[4] The pH of the lake remained low, near 5, so that the epilimnetic DIC concentration usually stayed near 20–40 μmoles/liter. Carbon depletion did not appear to be severe as in lake 227. In spite of this, epilimnetic standing crops of phytoplankton in lake 304 were lower (Fig. 5). As comparisons with data from lake 227 show, carbon did not increase standing crop beyond what would be expected from P and N additions alone. The added sucrose degraded rapidly to CO_2 (Thompson 1972; Thompson and Hamilton 1973).

---

[2] Microplankton is used here as a general term to apply to both algae and bacteria. The limits of 0.45 and 10 μ were the sizes of filters available for separating plankton.

[3] Removal $= \dfrac{F - \Delta M}{F}$, where F is the amount of element added as fertilizer and ΔM is the observed increase of element in the lake.

[4] The amount of added carbon is, of course, insignificant when compared to that metabolized by the lake in 1 yr. It is, however, of the order expected to enter a lake severely polluted by sewage.

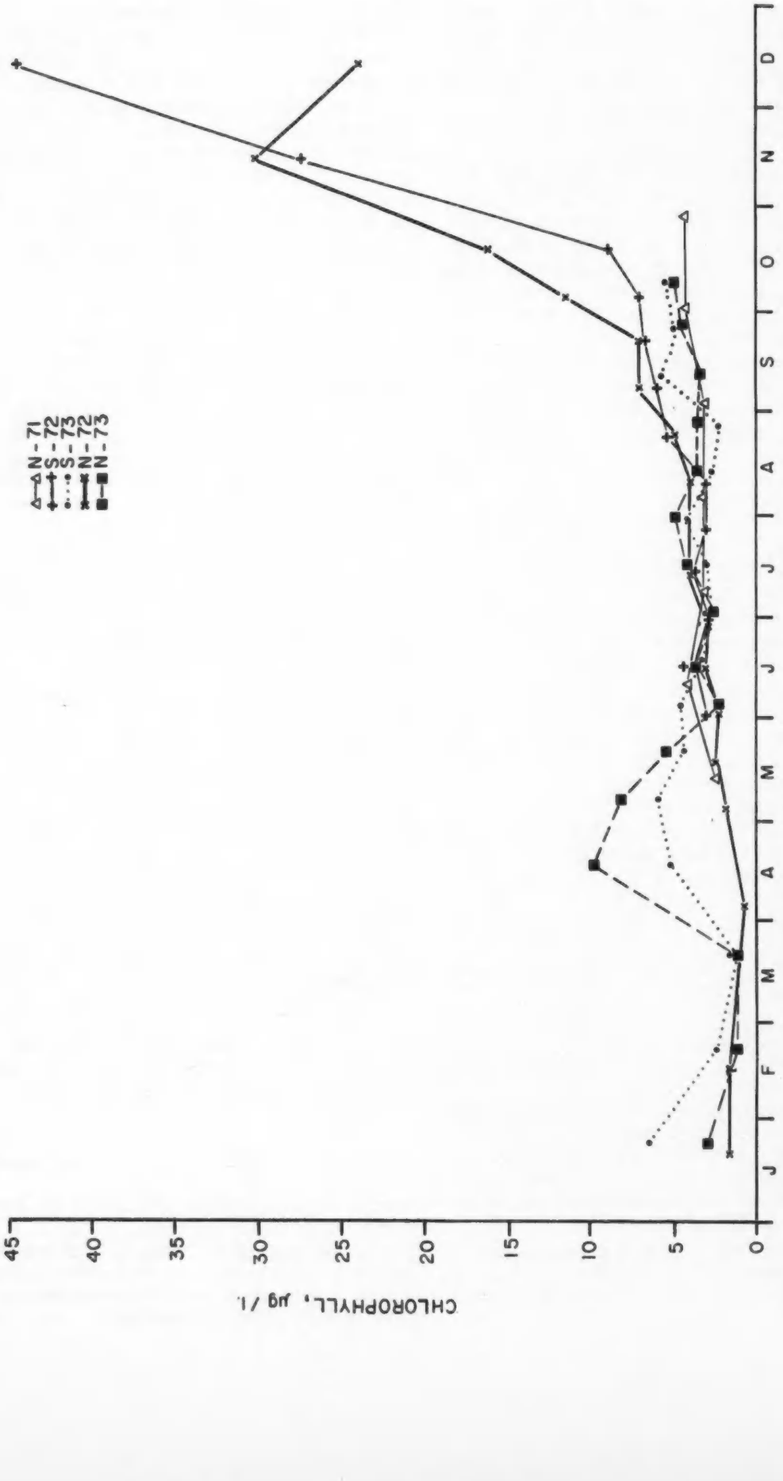


FIG. 3. Epilimnetic chlorophyll *a* in lake 302 before (1971) and during (1972–73) the hypolimnetic fertilization experiment. Lake 302 N was fertilized while 302 S was held as a control. Nutrient-rich effluents do not appear to cause severe algal blooms if added to the hypolimnion instead of to the epilimnion.

Because results of the CNP fertilization were negative, we decided to use the eutrophied lake no. 304 for a recovery experiment. Simulating a tertiary treatment operation, we eliminated phosphorus from the fertilization regime of the lake in 1973, while continuing to add nitrogen and carbon as in previous years. Phytoplankton standing crop declined immediately, with no bloom forming in 1973 (Fig. 5). The control of phosphorus inputs alone thus appears to be a realistic strategy for management of sewage-polluted lakes.

In another comparative study on a double basin lake (226, Fig. 1), we set up an experiment to test whether any effect on a natural lake could be ascribed to high inputs of nitrogen and carbon in the absence of phosphorus. One basin of the lake was enriched with nitrogen and carbon alone, the other with phosphorus, nitrogen, and carbon. Amounts were 0.60 g of PO_4–P, 3.2 g of NH_3–N, and 6.1 g of sucrose C/m^2 annually (north basin), and 3.2 g of NH_3–N and 6.1 g of C/m^2 per yr (south basin), applied to the epilimnion. The basin receiving phosphorus responded as expected, and that receiving only nitrogen and carbon showed no significant increase over the unfertilized condition (Fig. 6). Thus, in the presence of sufficient phosphorus, lakes of the area produce algal blooms rapidly. Without sufficient phosphorus, there is no detectable response.

As mentioned above, lake 227 was able to draw on atmospheric CO_2 to replenish its stock of DIC, allowing the lake to eutrophy in spite of its low initial carbon content. Some preliminary evidence suggested that the same might happen for nitrogen. Flett (1972) found that the amount of nitrogen gas added by bacterial fixation in lakes 227 and 304 was nearly as great as the nitrogen added as fertilizer. In 1971, 1 m diam columns that extended through the epilimnion, and enriched with phosphorus or phosphorus and carbon without nitrogen, produced standing crops equal to those enriched with phosphorus and nitrogen in combination, after a time lag of several weeks (Schindler unpublished data). *Anabaena*, a genus containing several nitrogen-fixing species, began to dominate the nitrogen-less tubes at the time the bloom began to form. Tubes which were fertilized with nitrogen, and those which received neither phosphorus nor nitrogen, did not have *Anabaena* blooms.

On the basis of the above observation, we decided to carry out another experiment, adding only phosphorus to a lake, hypothesizing that nitrogen-fixers would obtain enough nitrogen from the atmosphere to allow an algal bloom to develop.

Lake 261, with morphometry similar to lake 227, was chosen. This experiment is still in progress, and results have not yet been analyzed.

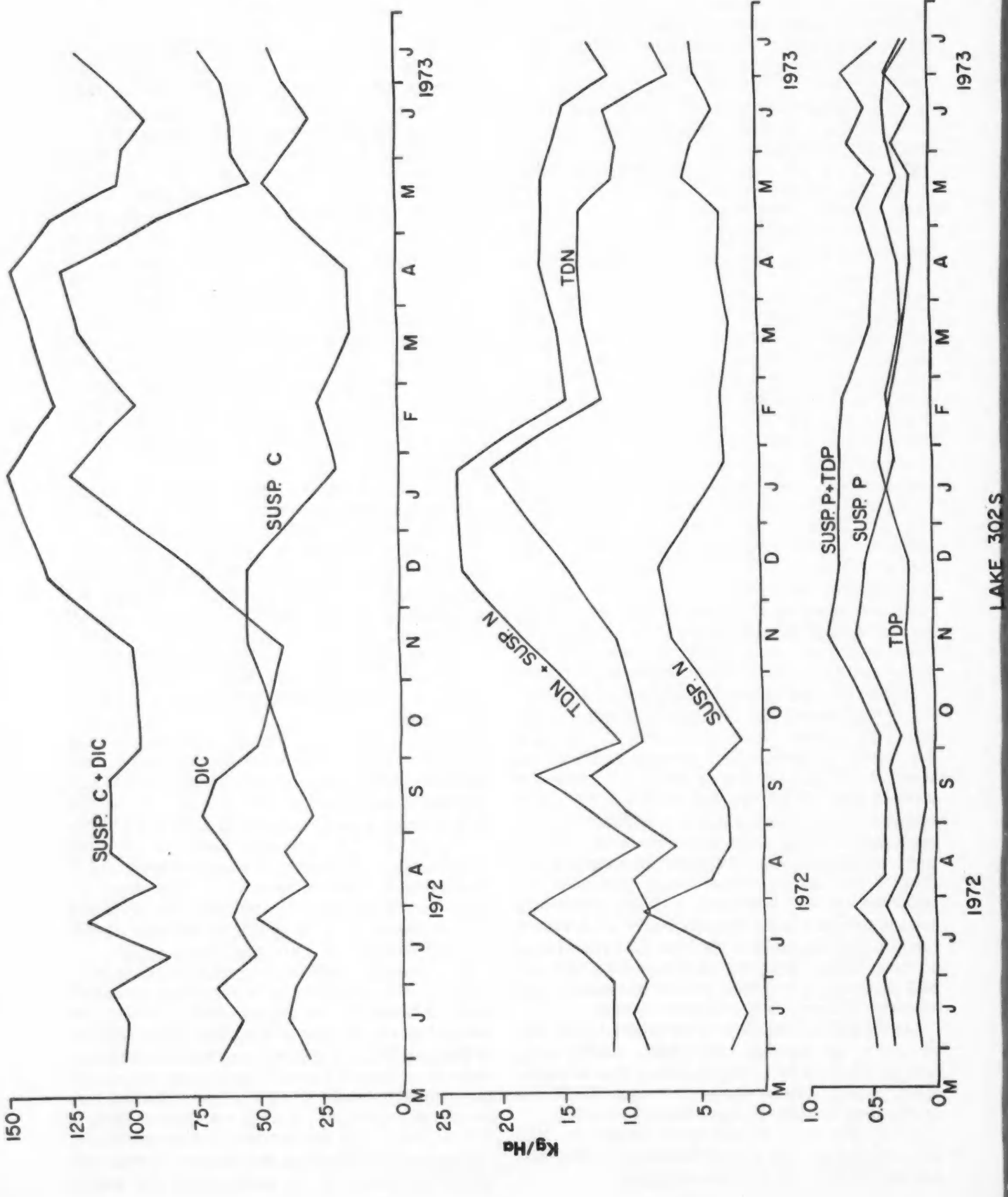
DEVELOPMENTS IN METHODOLOGY

In the course of whole-lake experiments, we found that the usual methods for making many biological and chemical measurements in lakes were inadequate for waters of the Canadian Precambrian Shield. For example, to measure primary production in oligotrophic lakes of the area, it was necessary to know the concentration of dissolved inorganic carbon (DIC). Early attempts to use alkalinity titrations failed, owing to the extremely low concentrations of DIC and high concentrations of interfering substances in some waters.

Stainton (1973) developed a gas-chromatographic technique for rapid sampling and analysis for low concentrations of DIC, using large syringes both for sample collection and as equilibration chambers during the analytical phase. This technique allows accurate measurements of primary production to be made, either by the ^{14}C technique (Schindler and Holmgren 1971; Schindler 1972; Fee 1973b) or by direct gas analysis (Schindler et al 1973a, c; Schindler and Fee 1973a, b).

Standard methods for measuring phosphate also proved too insensitive for use in ELA lakes. In both natural and artificially enriched lakes, concentrations of soluble reactive phosphorus were consistently undetectable (<0.7 μg/liter). Furthermore, tests utilizing radioactive phosphorus and Sephadex gel filtration showed that the molybdate method hydrolyzed phosphorus from colloidal material, so that the method greatly overestimated phosphate concentrations (see Rigler 1966, 1968). All modifications of the molybdate method were found to be deficient in this respect (M. P. Stainton unpublished data). Using bioassays (Rigler 1966) or Sephadex (Lean 1973), Schindler and Levine (unpublished data) found that concentrations of PO_4–P seldom exceeded 0.05 μg P/liter in any lake of the area during the ice-free season, including the highly eutrophic lake 227. Turnover times for this small concentration of phosphate were extremely rapid, as short as 1–2 min in lake 227 in midsummer. An entirely new approach to studying the dynamics of this element must be sought to interpret its role in algal nutrition in Canadian Shield waters.

In any study of effect of a perturbation on phytoplankton populations, it is important to obtain good information on phytoplankton production, because this is the rate process that links nutrients to biomass. Without accurate seasonal measurements there is no way of knowing whether an increase in standing crop is due to an increase in growth rate or to reduction of grazing and sedimentation. Yet we found that the standard in situ method for measuring phytoplankton production allowed only crude predictions to be made about the photo-


Kg/Ha
150
125
100
75
50
25
0
SUSP. C + DIC
DIC
SUSP. C
25
20
15
10
5
0
TDN + SUSP. N
TDN
SUSP. N
1.0
0.5
0
SUSP. P+TDP
SUSP. P
TDP
M J J A S O N D J F M A M J J
1972
1973
LAKE 302 S

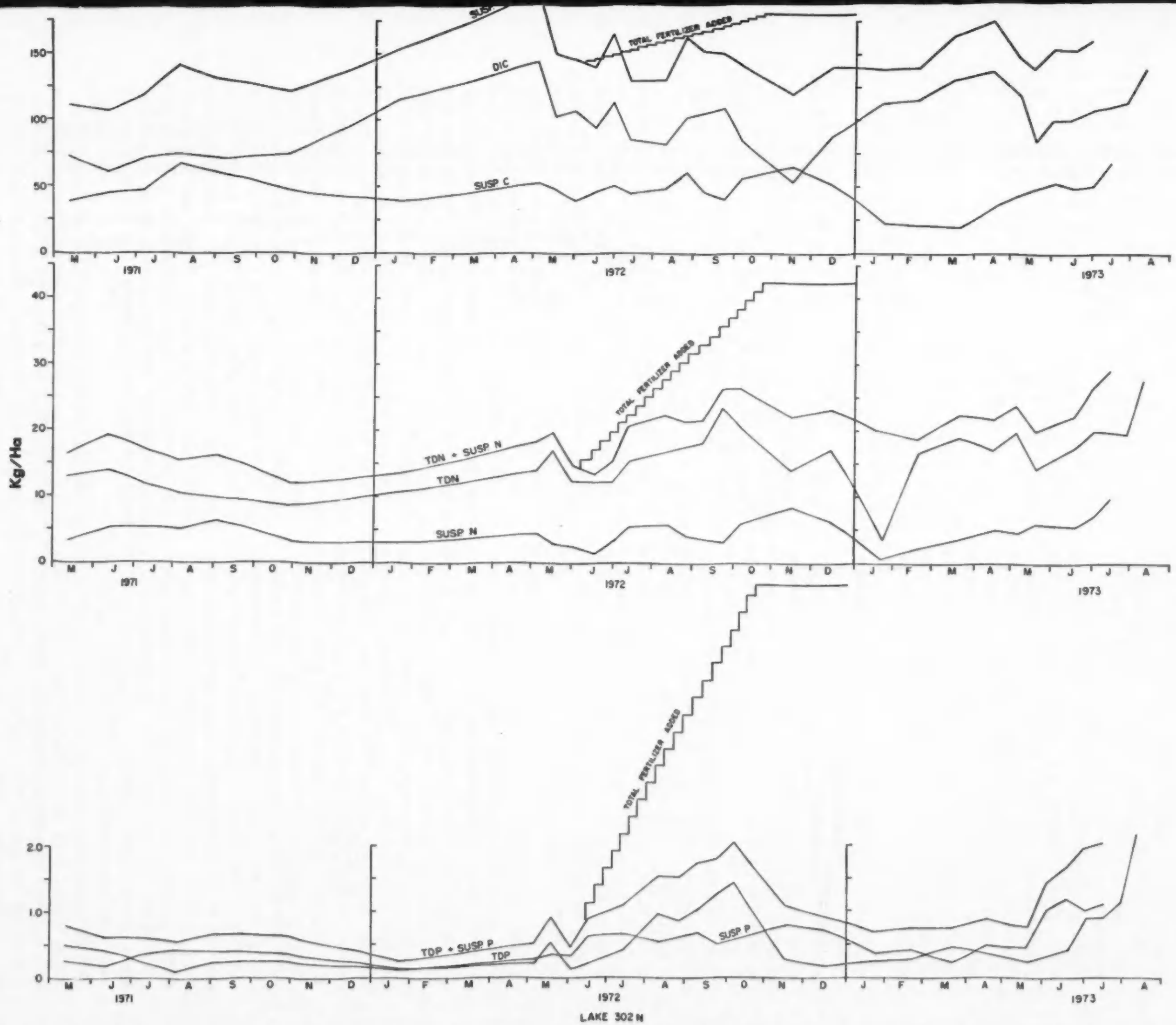


FIG. 4. Total mass of carbon (DIC = dissolved inorganic carbon), nitrogen (TDN = total dissolved nitrogen), and phosphorus (TDP = total dissolved phosphorus) in lake 302 N (fertilized) and 302 S (unfertilized). Dissolved organic carbon is not shown, because no significant changes were found during the study. Dissolved nutrients are quickly removed by seston (chiefly bacteria) and sedimented.

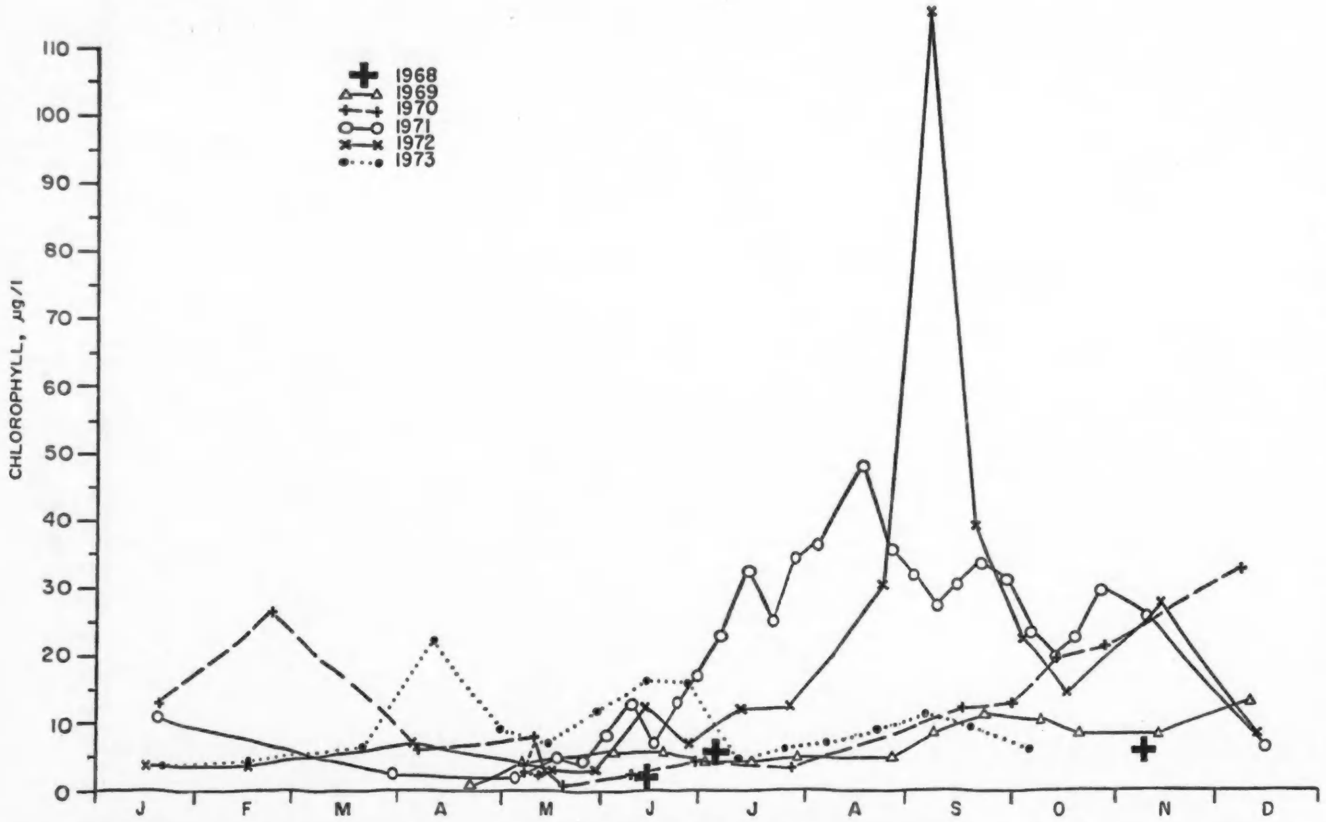


FIG. 5. Phytoplankton standing crop (as chlorophyll *a*) in the epilimnion of lake 304 before fertilization (1968, 1969, and 1970), during fertilization with P, N, and C (1971 and 1972) and while P is eliminated and fertilization with N and C is continued (1973). Results show the effectiveness of phosphorus control in eutrophication management.

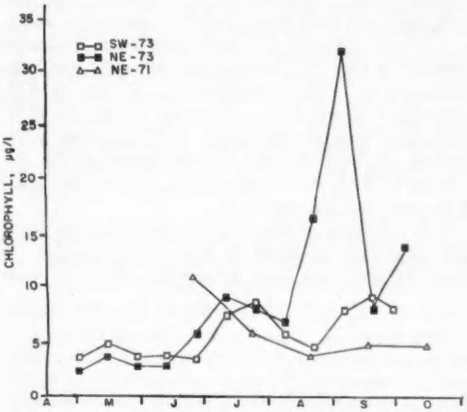


FIG. 6. Epilimnetic chlorophyll in lake 226 SW (fertilized with N and C in 1973) and in lake 226 NE (fertilized with P, N, and C in 1973). Without phosphorus algal standing crop will not respond to fertilization.

synthetic response of production in a lake ecosystem to treatments of various sorts. Extrapolation to periods with light intensities different from that during incubation is inaccurate as it does not take into account the logarithmic attenuation of light with depth, nor the exact nature of the light-production relationship for all depths in the euphotic zone. An incubator technique, coupled with numerical modelling methods for incorporating light and variation in photosynthetic capacity with depth, was developed by Fee (1969, 1973a) and extended to the Experimental Lakes (Fee 1973b). The method allows accurate prediction of primary production for any surface light distribution, facilitating comparisons of production in different lakes when measurements being compared are made on different days, in different years, or under different nutrient regimes. It has the advantage over earlier modelling techniques (Talling 1957; Vollenweider 1965) of incorporating natural surface light regimes, vertical inhomogeneities of light extinction, and algal biomass (Fee 1973b; Schindler and Fee 1973b). The method is especially useful for studying production in large waterbodies (Fee 1973a), because the ship can be underway while samples are being processed.

In addition to being more accurate for estimating seasonal rates of primary production, the incubator method has other advantages over in situ technique. As the rate of production is measured over a range of known irradiances, seasonal changes of photosynthetic parameters — such as the rate of production at optimum irradiance and the initial slope of the curve relating photosynthesis to light — can be quantitatively studied in relation to changes of nutrients, temperature, and surface light. Fee (1971), for example, showed that in Lake Michigan the initial slope of the photosynthesis vs. light curve dropped to very low values in midsummer in response to decreased nutrient availability (Fig. 7). This was largely responsible for the midsummer decline of integral photosynthesis because irradiances at and above the saturating rate occurred over only a shallow depth range during a brief part of the day. This same response to nutrient conditions occurs in ELA lakes (Fee unpublished data).

Work is now under way at the Experimental Lakes Area to define quantitatively the relation between known nutrient loading rates and the parameters of the photosynthesis vs. light curve. If successul, this will allow the prediction of rates of primary production in a lake of a hypothesized nutrient control scheme.

Reliable production estimates proved even more difficult to obtain in lake 227, where extreme DIC depletion was encountered during the midday period. Most of the DIC used by plankton for net photosynthesis during the midday period is drawn from the atmosphere. Because enclosure of phytoplankton communities in bottles eliminates this source of DIC, it is likely to cause production to be underestimated.

To overcome the above problems, a diurnal curve technique was developed, employing DIC measured by gas chromatography. Estimates of invasion of CO_2 to the lake plankton, of respiration, and of net production are obtained, as well as some idea of the time of day when maximum production occurs, and when DIC has been completely depleted (Schindler and Fee 1973b). The technique should prove useful both in enriched softwater lakes and in lakes where DIC has dwindled due to acid fallout from the atmosphere or from industrial pollution.

The lake 227 experiments clearly showed the importance of atmospheric CO_2 invasion in the carbon cycle of the lake. The diurnal curve technique mentioned above is not, however, sensitive enough to be used in large, turbulent, and unproductive waterbodies such as great lakes or oceans, where the difference in atmospheric and epilimnetic CO_2 concentrations is typically very small. High exchange rates of CO_2 and other gases may take place in spite of the low concentration gradient, due to the great turbulence of large waterbodies. Knowledge of atmospheric exchange rates for such waterbodies allows the role of the atmosphere in the aquatic carbon cycle to be evaluated, and provides useful information on the rate of dissipation of the excess atmospheric CO_2 produced by recent fossil fuel consumption (Broecker et al. 1971). CO_2 exchange measurements in such environments were originally made using ^{14}C fallout from atomic tests (Broecker 1963; Thurber and Broecker 1971; Munnich and Roether 1967). More recently, measurements using radon gas generated from the decay of natural radium (Broecker 1965; Broecker et al. 1967; Broecker and Peng 1971) or helium-3 generated by the decay of tritium (B. Clarke, McMaster University, unpublished data) have been used. Results of such studies can be used to estimate CO_2 invasion only if corrections can be made for hydroxylation-dehydroxylation reactions between CO_2 and dissolved ionic forms of carbon in water. Such "enhancement factors" have been evaluated directly in lake 227, where gas exchange has been measured by radon and helium, as well as CO_2 (Schindler et al. 1972; Emerson et al. 1973; T. Torgerson unpublished data). Once accurate information on such corrections is avaliable, the exchange of CO_2 and other gases may be predicted with considerable accuracy.

Interpretation of chemical dynamics in our small lakes was also hindered by lack of information on rates of diffusion and advection. Without such

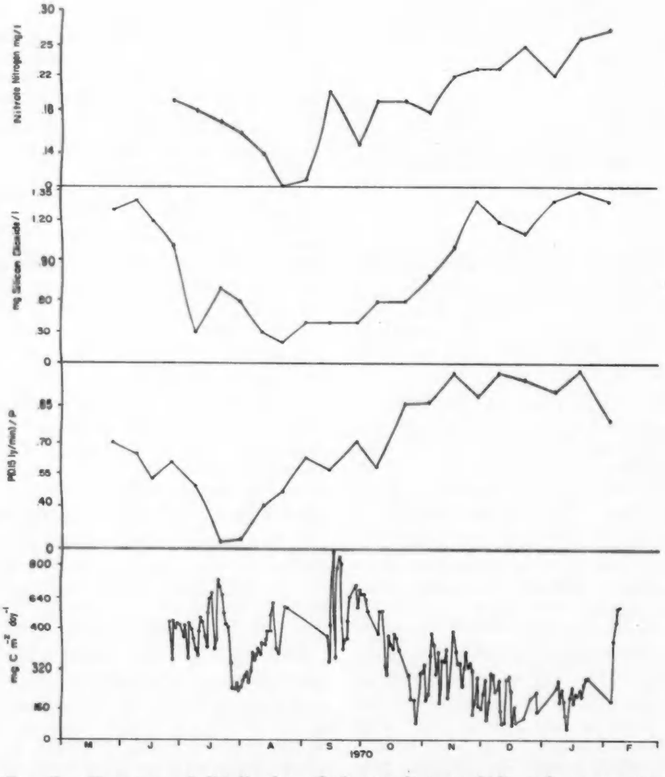


FIG. 7. The seasonal distribution of nitrate nitrogen, SiO_2, primary production at 0.015 ly/min divided by the light saturated rate, and integral production at a station 18 miles offshore in southern Lake Michigan. NO_3, SiO_2, and relative production were from epilimnion samples. Note the decline of relative production to very low levels in midsummer following the declining concentrations of NO_3 and SiO_2. This decline in relative production at low irradiances was responsible for the midsummer slump of integral production. As the thermocline dropped in the autumn, relative production increased following increasing concentrations of SiO_2 and NO_3. Low levels of integral production at this time resulted from low surface irradiances.

knowledge, it is impossible to evaluate the significance of nutrient exchange between epilimnion and hypolimnion, or between epilimnion and littoral zone. Current meters are of little use in such small lakes because of the low velocities involved. Temperature-dependent techniques have several flaws (Hutchinson 1957), and dye experiments must be done again and again to evaluate diffusion and advection over long periods.

Radon gas has proved useful for such studies, providing continuous estimates of diffusion from a single point source of radium for several months. The radium, which is susceptible to uptake by algae (Emerson and Hesslein 1973) is sealed in a PVC ampoule, covered by a piece of gas-permeable membrane. Radon gas passes through this membrane readily, and the parent radium is protected from algal uptake. Vertical, and horizontal (under ideal conditions), eddy diffusivity can be measured by the technique by suspending the radon-ampoule in a lake and measuring radon activity at set distances from it (Hesslein and Quay 1973). The technique is particularly advantageous under ice, as ampoule and sampling apparatus can be installed, then left until all disturbance due to installation has dissipated before measurements are begun.

Figure 8 illustrates how all the above studies can be fitted together to form a total picture of the carbon, phosphorus, and nitrogen cycles in one lake (227). Several facts of general significance are discernible, which would not be obvious from studies of concentrations of elements alone.

The rapid uptake, followed by high excretion of phosphate by microplankton, allows the maintenance of high standing crops of phytoplankton on extremely small concentrations of phosphate. Grazing and subsequent excretion by zooplankton also regenerates a significant amount of phosphate.

Carbon, too, maintains a high cycling rate with a very small reservoir of DIC, although turnover rates are somewhat lower than for phosphorus. The significant diurnal change in DIC reserves, which drop low enough to cause severe carbon deficiency in the phytoplankton for several hours at midday, is another salient feature. This condition is somewhat more extreme than in bicarbonate lakes of other regions, where DIC reserves would be 10–100 times higher.

The possible sources of input for different nutrient elements are of great significance from the management standpoint. Under natural conditions, supplies of phosphorus are limited to the small concentrations found in precipitation and runoff. Carbon, on the other hand, is to some degree available to the lake on demand by diffusion from the atmosphere. Unfertilized lakes usually maintain a slightly higher concentration of CO_2 gas than the atmosphere, probably due to influx and decomposition of allochthonous matter from the surrounding terrestrial drainage (Schindler et al. 1973c). Once fertilizers are added, however, this excess dissolved CO_2 and more from the atmosphere are required for algae to utilize the phosphorus and nitrogen supplied. Photosynthesis reduces epilimnetic DIC concentrations well below atmospheric levels, causing significant invasion of carbon from the atmosphere. This is rapidly fixed by algae so that it remains in the lake, causing a net increase in the carbon content of the lake. This will be retained permanently, provided enough cations are supplied by fertilizers to allow an increase in alkalinity.

The nitrogen cycle appears to be much like carbon. Nitrogen may be drawn from the atmosphere by algal or bacterial fixation to balance nutrient deficiencies which limit algal growth. Such fixation is, of course, limited by the development of an appropriate flora, so that the response of a lake to deficiencies may not be as immediate as to carbon shortages. The manager of lakes should note the facility with which lakes adjust to deficiencies of elements with atmospheric cycles. Control of carbon and nitrogen in effluents will not be effective, due to the impossibility of controlling these atmospheric exchanges.

Another important management consideration is the relative unimportance of outflow. In lake 227, with a water residence time of about 1 yr, only a small proportion of nutrient input is washed out the outflow, even when thermal stratification limits water exchange to the upper 2–3 m. Far more is lost to the littoral sediments and hypolimnion with sedimenting plankton. Unless a lake has a water renewal time of a few months or less, outflow will be a less important route for nutrient removal than sedimentation. Nutrients may therefore not be easily "flushed out" of most lakes of economic importance.

As plankton and other particulate matter fall through the water column they decay, releasing nutrients. Phosphorus appears to be almost immediately reused everywhere in the water column; nitrogen and carbon are not reutilized to the same degree in the hypolimnion, possibly because bacteria rather than algae are responsible for nutrient consumption. As a result, the C:N:P ratio in plankton decreases with depth, while the ratio in dissolved form increases (Fig. 9). Phosphorus is preferentially removed from the water column in this way, because plankton sinks to the lake bottom. It has not returned from hypolimnion sediments to any significant degree in the 5 yr the study has been under way. Carbon (chiefly CO_2 and methane) and nitrogen (chiefly ammonia), on the other hand, are released by

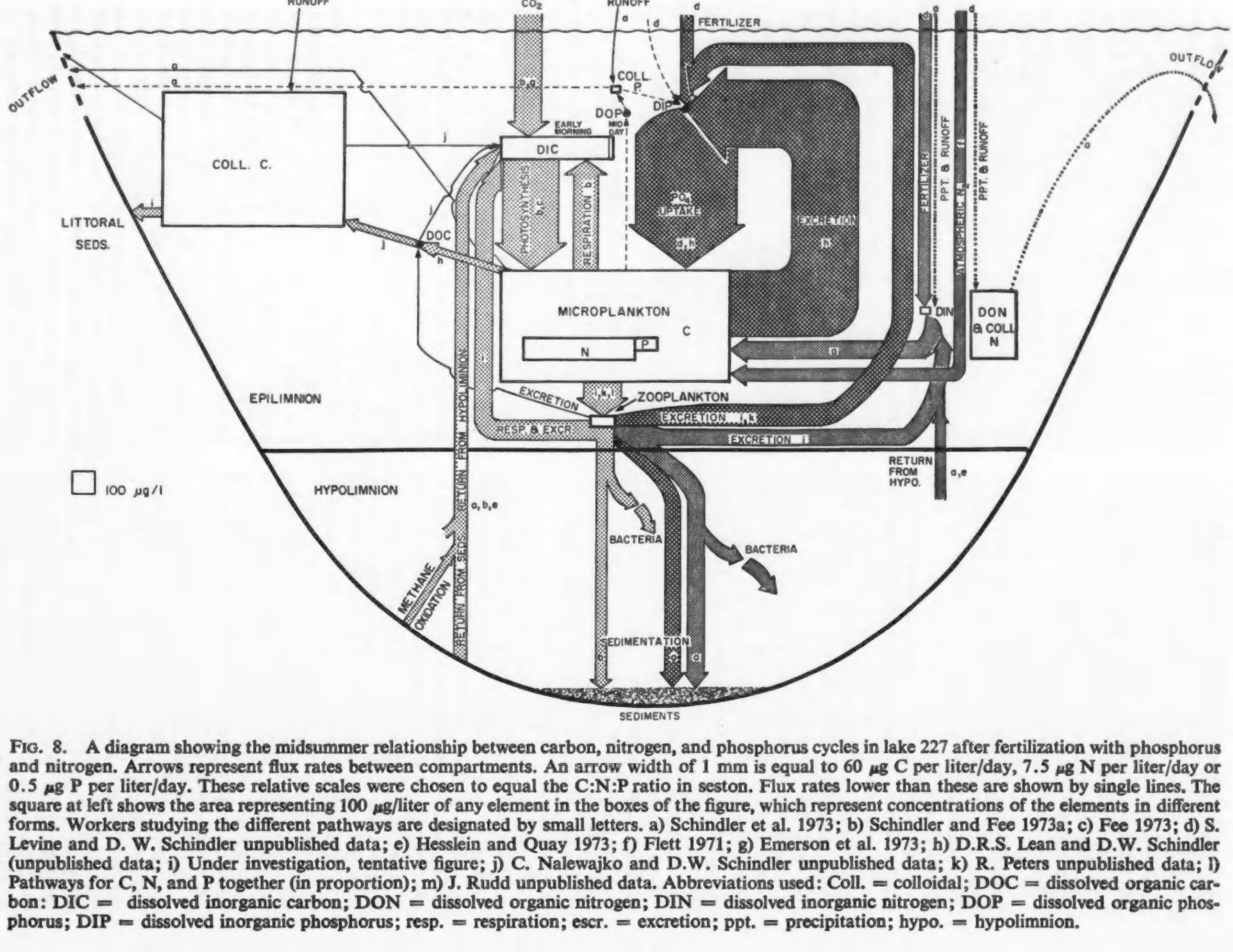

PPT & RUNOFF
ATMOSPHERIC CO2
PPT & RUNOFF
FERTILIZER
OUTFLOW
OUTFLOW
COLL. C.
COLL. P
DOP
DIP
EARLY MORNING
MID DAY
DIC
PHOTOSYNTHESIS b,f
RESPIRATION b
PO4 UPTAKE d,h
EXCRETION h
FERTILIZER
PPT. & RUNOFF
ATMOSPHERIC N2
PPT. & RUNOFF
DIN
DON & COLL N
MICROPLANKTON
C
N
P
DOC
LITTORAL SEDS.
EPILIMNION
HYPOLIMNION
100 µg/l
EXCRETION
ZOOPLANKTON
RESP. & EXCR
EXCRETION i,k
EXCRETION i
RETURN FROM HYPO.
RETURN FROM HYPOLIMNION
RETURN FROM SEDS.
a,b,e
a,e
METHANE
OXIDATION
BACTERIA
BACTERIA
SEDIMENTATION
SEDIMENTS

FIG. 8. A diagram showing the midsummer relationship between carbon, nitrogen, and phosphorus cycles in lake 227 after fertilization with phosphorus and nitrogen. Arrows represent flux rates between compartments. An arrow width of 1 mm is equal to 60 µg C per liter/day, 7.5 µg N per liter/day or 0.5 µg P per liter/day. These relative scales were chosen to equal the C:N:P ratio in seston. Flux rates lower than these are shown by single lines. The square at left shows the area representing 100 µg/liter of any element in the boxes of the figure, which represent concentrations of the elements in different forms. Workers studying the different pathways are designated by small letters. a) Schindler et al. 1973; b) Schindler and Fee 1973a; c) Fee 1973; d) S. Levine and D. W. Schindler unpublished data; e) Hesslein and Quay 1973; f) Flett 1971; g) Emerson et al. 1973; h) D.R.S. Lean and D.W. Schindler (unpublished data; i) Under investigation, tentative figure; j) C. Nalewajko and D.W. Schindler unpublished data; k) R. Peters unpublished data; l) Pathways for C, N, and P together (in proportion); m) J. Rudd unpublished data. Abbreviations used: Coll. = colloidal; DOC = dissolved organic carbon: DIC = dissolved inorganic carbon; DON = dissolved organic nitrogen; DIN = dissolved inorganic nitrogen; DOP = dissolved organic phosphorus; DIP = dissolved inorganic phosphorus; resp. = respiration; escr. = excretion; ppt. = precipitation; hypo. = hypolimnion.

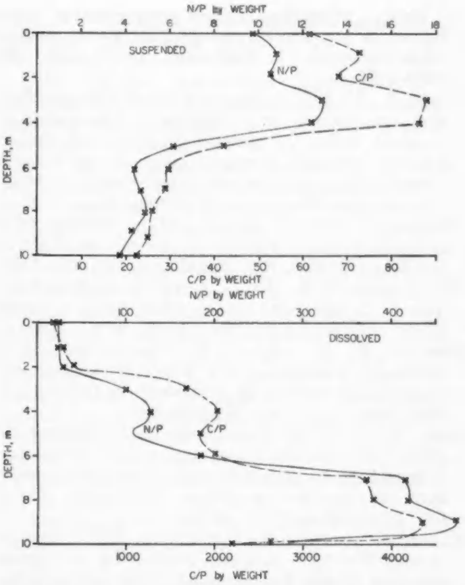


FIG. 9. Changes in C:P and N:P ratios in seston and dissolved substances with depth, lake 227, August 1972, illustrating the loss of C and N relative to P by decomposition in the water column during summer.

decomposition both in sediments and hypolimnion. The result is a great increase in concentration of dissolved forms of these two elements in the hypolimnion, and subsequent diffusion back to the epilimnion, where they can be reutilized by plankton. From the standpoint of both atmospheric exchange and hypolimnetic feedback, phosphorus appears to be far easier to control than nitrogen or carbon, because it is much less affected by atmospheric exchange and hypolimnetic feedback. The effectiveness of phosphorus control programs in reducing eutrophication is demonstrated by the lake 304 and 226 experiments above.

The above studies illustrate the complexity likely to be encountered when causes for and mechanisms controlling phenomena observed in lakes are sought. Even when several extremely important factors, such as water renewal time and amount and timing of nutrient input are known to within a few percent, it is difficult to unravel the complex series of events which govern even the simplest qualitative and quantitative changes in the chemistry and biology of lakes. Yet unless causes and mechanisms are known and understood, attempts at management of lakes will be extremely unreliable, as 15th century attempts to control plague and cholera must have been. Experimental lakes offer an opportunity to test theories developed in the laboratory, as well as to question and probe hypotheses resulting from purely observational studies in relatively uncontrolled water bodies.

EFFECTS OF MANAGEMENT PRACTICES ON PRECAMBRIAN SHIELD WATERSHEDS

One of the first programs begun at ELA was the Kenora Research Watershed study, a concerted attempt to evaluate the importance of streamflow, groundwater, and precipitation on the hydrological and chemical regimes of natural watersheds in the area, to provide baseline information for studies involving manipulation of the chemical or hydrological regimes (Armstrong and Schindler 1971; Barica and Armstrong 1971; Lerman and Brunskill 1971; Newbury et al. 1974; Bottomley et al. 1974a, b; Schindler et al. 1973d). Personnel from the University of Manitoba, Water Survey of Canada, Canadian Meteorological Service, and Canada Centre for Inland Waters have cooperated with ELA personnel in these studies.

In 1971, a joint project was undertaken by ELA staff and the Canadian Forestry Service to evaluate the effects of clear-cutting of forests, as practiced by the pulp and paper industry, and other activities associated with logging in the Canadian Shield, such as road building, scarification, and slash burning. The quantity and chemistry of runoff is being compared before and after logging, in a manner similar to that used by Likens and colleagues at Hubbard Brook, New Hampshire (Likens et al. 1970). If clear-cutting causes increased losses of nutrients, both deterioration of forest soils and potential eutrophication problems will be evaluated. In addition, the localized movement of nutrients in soils and the effect of various post-logging treatments on forest regeneration are being evaluated. Long-term plans are to evaluate other human activities important on the Canadian Shield, suc has forest fertilization, cottage building, fallout of acid and heavy metals from smelters, and application of biocides or forest-fire retardants. The overall purpose of this program is to provide a solid back-ground of data upon which sound policies for management of Canadian Shield resources can be based.

Although they cannot provide all the answers, whole-ecosystem experiments of the sort described here can provide scientific evidence which it may be impossible to obtain in laboratory systems or large, uncontrolled ecosystems. We have provided only a few preliminary examples. If used properly, experimental lakes and watershed can play a role as indispensable in modern water management as experiment stations have played in development of modern agricultural management practices.

Anon. 1970. We hung phosphates without a fair trial. Can. Res. Dev. March–April. p. 19–42.

Armstrong, F. A. J., and D. W. Schindler. 1971. Preliminary characterization of waters in the Experimental Lakes Area, northwestern Ontario. J. Fish. Res. Board Can. 28: 171–187.

Barica, J., and F. A. J. Armstrong. 1971. Contribution by snow to the nutrient budget of some small northwestern Ontario lakes. Limnol. Oceanogr. 16: 891–899.

Bottomley, D. J., J. A. Cherry, and K. G. Kennedy. 1974a. Geohydrologic studies in a small Precambrian Shield watershed, northwestern Ontario. 2. Chemical weathering rates and process. (In preparation)

Bottomley, D. J., J. A. Cherry, and R. W. Newbury. 1974b. Geohydrologic studies in a small Precambrian Shield watershed, northwestern Ontario. 3. Hydrochemical interpretations of storm runoff processes. (In preparation)

Broecker, W. S. 1963. Radioisotopes and large scale oceanic mixing, p. 88–108. *In* M. N. Hill [ed.] The sea. Vol. 2. John Wiley and Sons Ltd., London.

1965. An application of natural radon to problems in ocean circulation, p. 116–145. *In* Symposium on Diffusion in Oceans and Fresh Waters. Lamont Geological Observatory (1964), Palisades, N.Y.

Broecker, W. S., Y.-H. Li, and J. Cromwell. 1967. Radium-226 and radon-222: concentration in Atlantic and Pacific oceans. Science 158: 1307–1310.

Broecker, W. S., Y.-H. Li, and T.-H. Peng. 1971. Carbon dioxide — man's unseen artifact, p. 287–324. *In* D. W. Hood [ed.] Impingement of man on the oceans. Wiley Interscience, N.Y.

Broecker, W. S., and T.-H. Peng. 1971. The vertical distribution of radon in the BOMEX area. Earth Planet. Sci. Lett. 11: 99–108.

Brunskill, G. J., and D. W. Schindler. 1971. Geography and bathymetry of selected lake basins, Experimental Lakes Area, northwestern Ontario. J. Fish. Res. Board Can. 28: 139–155.

Emerson, S., W. S. Broecker, and D. W. Schindler. 1973. Gas exchange rates in a small lake as determined by the radon method. J. Fish. Res. Board Can. 30: 1475–1484.

Emerson, S., and R. Hesslein. 1973. The distribution and uptake of artificially introduced radium-226 in a small lake. J. Fish. Res. Board Can. 30: 1485–1490.

Fee, E. J. 1969. A numerical model for the estimation of photosynthetic production, integrated over time and depth, in natural waters. Limnol. Oceanogr. 14: 906–911.

1971. A numerical model for the estimation of integral primary production, and its application to Lake Michigan. Ph.D. Thesis. Univ. Wisconsin, Madison, Wis. 169 p.

1973a. A numerical model for determining integral primary production and its application to Lake Michigan. J. Fish. Res. Board Can. 30: 1447–1468.

1973b. Modelling primary production in water bodies: a numerical approach that allows vertical inhomogeneities. J. Fish. Res. Board Can. 30: 1469–1473.

Flett, R. J. 1972. Measurement of nitrogen fixation rates by acetylene reduction and estimation of seasonal inputs of biologically fixed nitrogen to several artificially fertilized lakes in the Experimental Lakes Area of northwestern Ontario. M.Sc. Thesis. Univ. Manitoba, Winnipeg, Man. 102 p.

Hesslein, R., and P. Quay. 1973. Vertical eddy diffusion studies in the thermocline of a small stratified lake. J. Fish. Res. Board Can. 30: 1491–1500.

Hutchinson, G. E. 1957. A treatise on limnology. Vol. 1. Geography, physics and chemistry. John Wiley and Sons Ltd., New York, N.Y. 1015 p.

Johnson, W. E., and J. R. Vallentyne. 1971. Rationale, background and development of experimental lake studies in northwestern Ontario. J. Fish. Res. Board Can. 28: 123–128.

Kerr, P. C., D. F. Paris, and D. L. Brockway. 1970. The interrelation of carbon and phosphorus in regulating heterotrophic and autotrophic populations in aquatic ecosystems. U.S. Gov. Print. Off. Washington, D.C. 53 p.

Kling, H. J., and S. K. Holmgren. 1972. Species composition and seasonal distribution of phytoplankton in the Experimental Lakes Area, northwestern Ontario. Fish. Res. Board Can. Tech. Rep. 337: 51 p.

Kuentzel, L. E. 1969. Bacteria, carbon dioxide and algal blooms. J. Water Pollut. Control Fed. 41: 1737–1747.

Lange, W. 1967. Effects of carbohydrates on the symbiotic growth of planktonic blue-green algae with bacteria. Nature 215: 1277–1278.

1970. Cyanophyta–bacteria systems: effects of added carbon compounds or phosphate an algal growth at low nutrient concentrations. J. Phycol. 6: 230–234.

Lean, D. R. S. 1973. Phosphorus movement between biologically important compartments in lake water. J. Fish. Res. Board Can. 30: 1525–1536.

Lerman, A., and G. J. Brunskill. 1971. Migration of major constituents from lake sediments into lake water and its bearing on lake water composition. Limnol. Oceanogr. 16: 880–890.

Likens, G. E., F. H. Bormann, N. M. Johnson, D. W. Fisher, and R. S. Pierce. 1970. Effect of forest cutting and herbicide treatment on nutrient budgets in the Hubbard Brook watershed-ecosystem. Ecol. Monogr. 40: 23–47.

Munnich, K. O., and W. Roether. 1967. Transfer of bomb C-14 and tritium from the atmosphre to the ocean. Internal mixing of the ocean on the basis of tritium and C-14 profiles, p. 93–104. *In* Radioactive dating and low level counting. I.A.E.A. Vienna.

Newbury, R. W., K. G. Beatty, and J. A. Cherry. 1974. Geohydrologic studies in a small Precambrian Shield watershed, northwestern Ontario. 1. Water budgets of a lake and terrestrial subbasins. (In preparation)

Rigler, F. H. 1966. Radiobiological analysis of inorganic phosphorus in lakewater. Verh. Int. Ver. Limnol. 16: 465–470.

1968. Further observations inconsistent with the hypothesis that the molybdenum blue method measures orthophosphate in lake water. Limnol. Oceanogr. 13: 7–13.

Rudd, J. W. M., and R. D. Hamilton. 1973. The measurement of adenosine triphosphate (ATP) in two Precambrian Shield lakes of northwestern Ontario. J. Fish. Res. Board Can. 30: 1537–1546.

Schindler, D. W. 1972. Production of phytoplankton and zooplankton in Canadian Shield lakes, p. 311–332. *In* Z. Kajak and A. Hillbricht-Ilkowska [ed.] Proceedings, IBP-UNESCO Symposium on Productivity Problems of Freshwaters, Kazimierz Dolny, Poland, May 6–12, 1970.

Schindler, D. W., F. A. J. Armstrong, S. K. Holmgren, and G. J. Brunskill. 1971. Eutrophication of lake 227, Experimental Lakes Area, northwestern Ontario, by addition of phosphate and nitrate. J. Fish. Res. Board Can. 28: 1763–1782.

Schindler, D. W., G. J. Brunskill, S. E. Emerson, W. S. Broecker, and T.-H. Peng. 1972. Atmospheric carbon dioxide: its role in maintaining phytoplankton standing crops. Science 177: 1192–1194.

Schindler, D. W., and E. J. Fee. 1973a. Diurnal variation of dissolved inorganic carbon and its use in estimating primary production and CO_2 invasion in lake 227. J. Fish. Res. Board Can. 30: 1501–1510.

1973b. The roles of nutrient cycling and radiant energy in aquatic communities. *In* J. P. Cooper [ed.] Proceedings, IBP Symposium on the Roles of CO_2 and Radiant Energy in Photosynthetic Production, Aberystwyth, Wales, April 1973.

Schindler, D. W., V. E. Frost, and R. V. Schmidt. 1973a. Production of epilithiphyton in two lakes of the Experimental Lakes Area, northwestern Ontario. J. Fish. Res. Board Can. 30: 1511–1524.

Schindler, D. W., and S. K. Holmgren. 1971. Primary production and phytoplankton in the Experimental Lakes Area, northwestern Ontario, and other low-carbonate waters, and a liquid scintillation method for determining ^{14}C activity in photosynthesis. J. Fish. Res. Board Can. 28: 189–201.

Schindler, D. W., H. Kling, R. V. Schmidt, J. Prokopowich, V. E. Frost, R. A. Reid, and M. Capel. 1973b. Eutrophication of lake 227 by addition of phosphate and nitrate. The second, third, and fourth years of enrichment, 1970, 1971, and 1972. J. Fish. Res. Board Can. 30: 1415–1440.

Schindler, D. W., D. R. S. Lean, and E. J. Fee. 1973c. Nutrient cycles in freshwater ecosystems. *In* D. E. Reichle [ed.] Proceedings IBP Symposium on Productivity of World Ecosystems, Seattle, Washington, Sept. 1972. (In press)

Schindler, D. W., R. W. Newbury, and J. A. Cherry. 1973d. Nutrient regimes and geochemical weathering processes in the Rawson Lake (lake 239) watershed, Experimental Lakes Area. Fish. Res. Board Can. Tech. Rep. (In press)

Stainton, M. P. 1973. A syringe gas-stripping procedure for gas-chromatographic determination of dissolved inorganic and organic carbon in fresh water and carbonate in sediments. J. Fish. Res. Board Can. 30: 1441–1445.

Talling, J. F. 1957. Photosynthetic characteristics of some freshwater plankton diatoms in relation to underwater radiation. New Phytol. 56: 29–50.

Talling, J. F., R. B. Wood, M. V. Prosser, and R. M. Baxter. 1973. The upper limit of photosynthetic productivity by plankton: evidence from Ethiopian soda lakes. Freshwater Biol. 3: 53–76.

Thompson, B. M. 1972. Heterotrophic utilization of sucrose in an artificially enriched lake. M.Sc. Thesis. Univ. Manitoba, Winnipeg, Man. 92 p.

Thompson, B. M., and R. D. Hamilton. 1973. Heterotrophic utilization of sucrose in an artificially enriched lake. J. Fish. Res. Board Can. 30: 1547–1552.

Thurber, D. L., and W. S. Broecker. 1971. The behaviour of radiocarbon in the surface waters of the Great Basin. *In* I. U. Olsson [ed.] Nobel Symp. 12, Radiocarbon Variations and Absolute Chronology. p. 379.

Vollenweider, R. A. 1965. Calculating models of photosynthesis-depth curves and some implications regarding day rate estimates in primary production measurements. Mem. Ist. Ital. Idrobiol. Dott. Marco de Marchi Pallanza, Italy (Suppl.) 18: 425–457.

Recent Limnological Studies of Okanagan Basin Lakes and their Contribution to Comprehensive Water Resource Planning[1]

J. G. STOCKNER

Department of the Environment, Fisheries and Marine Service
Pacific Environment Institute, West Vancouver, B.C.

AND T. G. NORTHCOTE

Institute of Animal Resource Ecology
University of British Columbia, Vancouver 8, B.C.

STOCKNER, J. G., AND T. G. NORTHCOTE. 1974. Recent limnological studies of Okanagan Basin lakes and their contribution to comprehensive water resource planning. J. Fish. Res. Board Can. 31: 955–976.

Results of limnological investigations of Okanagan mainstem and headwater lakes are reviewed in relation to their input to studies of comprehensive water resource management in the Okanagan Valley, British Columbia. The current trophic state of the lakes is discussed on the basis of our understanding of their current condition and areal annual loads of total phosphorus. The practical usefulness of limnological data in this multidisciplinary study is reviewed, and specific investigations are discussed in relation to their essential and nonessential components, and how these have or have not contributed to the development of management strategies. The role of limnologists in this type of applied study is discussed and their cooperation in similar types of studies is encouraged.

STOCKNER, J. G., AND T. G. NORTHCOTE. 1974. Recent limnological studies of Okanagan Basin lakes and their contribution to comprehensive water resource planning. J. Fish. Res. Board Can. 31: 955–976.

Nous passons en revue les résultats de recherches limnologiques effectuées dans la branche principale de l'Okanagan et des lacs de la tête des eaux en relation avec l'apport qu'elles fournissent aux études d'aménagement global des ressources aquatiques de la vallée de l'Okanagan, Colombie-Britannique. Nous examinons l'état trophique actuel des lacs dans le contexte de notre compréhension de leur condition présente et des charges annuelles, par superficie, de phosphore total. Nous passons en revue l'utilité pratique des données limnologiques dans cette étude multidisciplinaire et analysons des recherches spécifiques en rapport avec leurs composants essentiels et non essentiels, et la façon dont elles ont contribué ou non à l'élaboration de plans d'action pour la gestion. Nous discutons du rôle des limnologues dans ce type de recherches appliquées et les encourageons à collaborer à ce genre d'études.

Accepted December 12, 1973

THE Okanagan Basin in British Columbia, Canada, is a fertile valley containing five major lakes, interconnected by river flow. Okanagan Lake is the largest, over 93 km long and serving as a large reservoir for the valley. The replenishment of water to lakes of the Okanagan Basin is irregular, owing to extreme year-to-year variation in runoff. Growing demands for water in recent years, coupled with shortages, have increased conflicts among users. Added to this situation are further problems concerning disposal of wastes, which have led to a serious degradation of surface water quality. These water resource problems have been a matter of particular concern to local residents and to the general public at large. Water quality deterioration, together with increased water demands by agriculture, industry, and a growing population, have jeopardized an economy heavily dependent on water based tourism and recreational activities.

The complexity of these problems, plus a wide range of planning alternatives, brought about a joint Federal–Provincial Okanagan Basin Study

---

[1] This paper, part of a special issue that comprises a comprehensive review of Limnology in Canada, was prepared to mark the 19th Congress of the International Association of Limnology (SIL), in Winnipeg, Man., during August 1974.

Printed in Canada (J3244)

Agreement — a study to develop and test techniques for comprehensive inter-jurisdictional water resource planning. The Agreement was signed in 1969 by both governments and $2 million was allocated for a 4-yr study. The study, involving both water quality and quantity problems, required inputs from a wide range of scientific disciplines, including limnology. Chemical, physical, geological, and biological limnological studies were conducted, with greatest emphasis placed on biological aspects.

The primary objective of this paper is to discuss salient findings of limnological studies, especially those of significance when water resource planning alternatives were formulated at later stages in the study. Rhode (1969a) has strongly emphasized the urgent need of limnologists to participate in multidisciplinary programs designed to manage the water resource. The management of any resource, and especially the water resource, must be based on a good foundation of limnological research. For this reason it is important for the limnologists to communicate with decision makers, so that the relevancy of limnological research to water management problems can find direct application to general social betterment. What follows, therefore, is a synopsis of basic findings of the Okanagan Basin limnology program, with a discussion of how these have had direct application to the development of water management alternatives and how they might have had more.

There has been a paucity of previous limnological work on Okanagan Basin lakes. In 1935, Rawson (Clemens et al. 1939) conducted a general limnological survey of Okanagan, Wood, and Kalamalka lakes, results of which have proved useful to current investigations. In 1948, Ferguson (1949) conducted a survey of Skaha Lake, and this study too has served as valuable background information. Stein and Coulthard (1971) and Coulthard and Stein (1969) have conducted broad limnological studies of Okanagan lakes. Their studies preceded the joint Federal–Provincial Okanagan Basin Agreement, and provided insight into potential water quality problem areas, as well as tentatively identifying nutrient sources causing current problems.

Description of Study Area

GEOLOGICAL SETTING

The Okanagan Valley is a structural trench overlying a system of subparallel, linked faults that separate the late Paleozoic or early Mesozoic Monashee group of metamorphic rocks of differing lithology, but of similar age. This trench is partially filled by several hundred meters of unconsolidated materials of varying thickness. It is likely that the unconsolidated material was deposited in association with earlier glaciations of the Pleistocene epoch. The nature of the deposits is uncertain, but it seems probable that during and after the Pleistocene, the valley was the site of deposition, resulting from glacial outwash, direct glaciation, and lacustrine fluvial sedimentation (Nasmith 1962; St. John et al. 1973). During deglaciation a number of terraces were formed as the lowering of postglacial lake levels was repeatedly arrested.

PHYSIOGRAPHY

The Okanagan River drainage extends from north latitude 50° 50′ in close proximity to Shuswap Lake, and flows in a southerly direction about 204 km in Canada and 117 km in the United States, where it joins the Columbia River system. The mainstem system is comprised of six lakes all connected by river flow (Fig. 1). The Wood–Kalamalka lakes sub-basin discharges via Vernon Creek to the Vernon arm of Okanagan Lake (mean annual discharge 21.3×10^6 m^3). The outflow of Okanagan Lake becomes the Okanagan River (mean annual discharge 439.0×10^6 m^3), flows to the south and interconnects Skaha, Vaseux, and Osoyoos lakes. From Wood Lake to Osoyoos Lake the elevation drops 133 m, from 391 to 278 m MSL.

The Okanagan Valley is U-shaped with mountains rising 100–2500 m on both sides. Over 100 headwater lakes occur in the drainage basin at elevations to 1951 m. These lakes provide some storage for the mainstem lakes as well as supporting valuable sports fisheries. Benchlands perched 30–70 m above the main lakes are a conspicuous feature of valley topography. The soil of the benchlands is ideally suited for fruit crops; bottomlands adjacent to the Okanagan River are used chiefly for dairy farming. The higher, open forest lands are grass-covered and serve as valuable open range for cattle summer grazing.

While the entire valley lies in a dry belt, there is a gradual change in climatic conditions from south to north. At Oliver, located in the extreme southern portion of the valley, average rainfall is 27.5 cm yr^{-1} (10.8 in), and at Armstrong, in the extreme northern end of the valley it is 44 cm yr^{-1} (17.2 in). Maximum temperatures in July–August may reach 43 C (110 F), and minimums of -27 C (-20 F) are not uncommon in January. There are approximately 162 frost-free days at Oliver, but only 107 at Armstrong.

Most of the mainstem lakes have an ice cover in winter, commencing generally in late December and lasting until the middle of March. Okanagan Lake, because of its size (93 km) seldom has a complete ice cover, although bays and shallow arms are often ice-covered for long periods.

The majority of inflow water to the lakes comes during a 3-mo period from April to June. Except for major tributary streams, most small stream beds are dry from July to November, a result of upstream storage on regulated headwater lakes and land irrigation requirements. It is estimated that of a net annual inflow of 439×10^6 m^3 to Okanagan Lake, up to 75% is

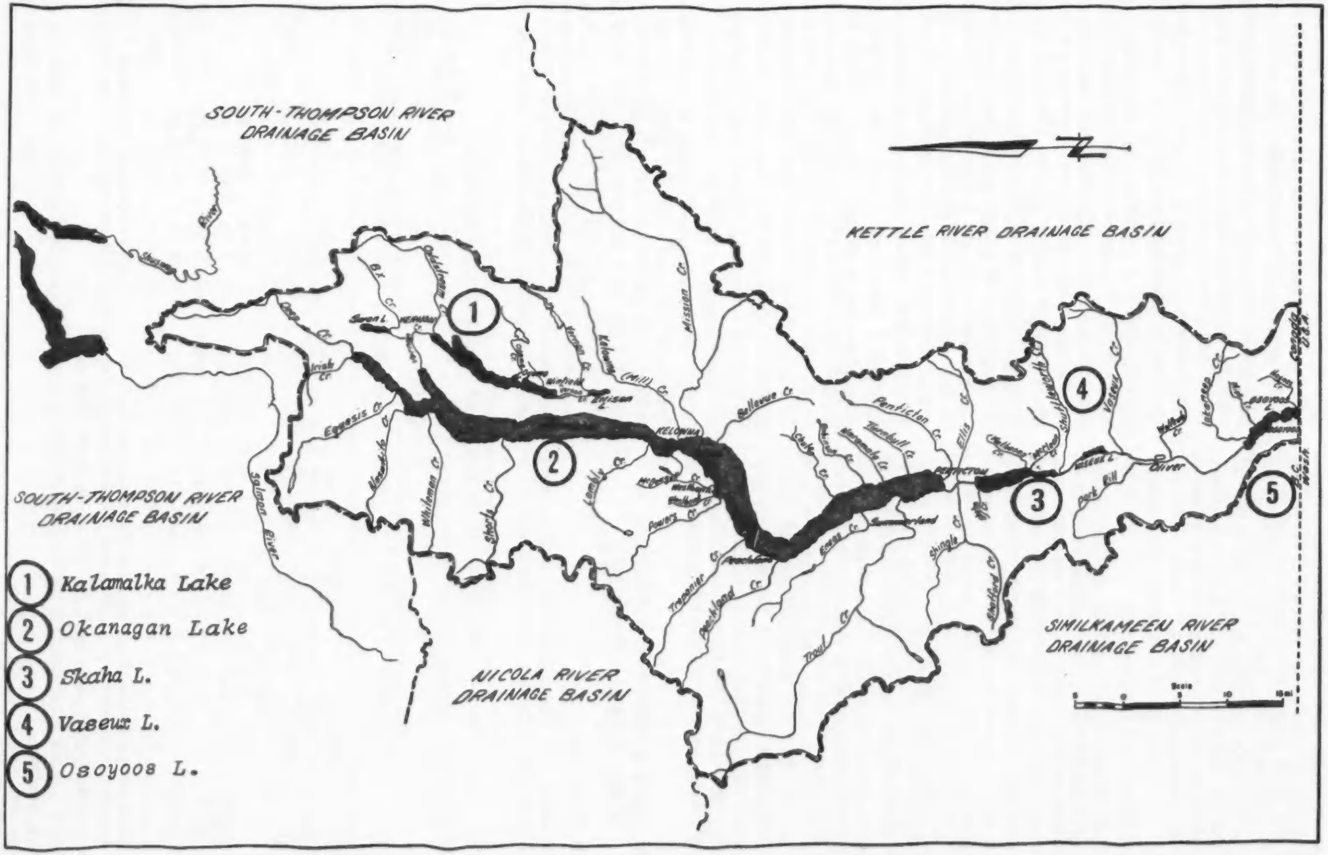

SOUTH-THOMPSON RIVER DRAINAGE BASIN
KETTLE RIVER DRAINAGE BASIN
SOUTH-THOMPSON RIVER DRAINAGE BASIN
NICOLA RIVER DRAINAGE BASIN
SIMILKAMEEN RIVER DRAINAGE BASIN
Shuswap River
Deep Cr.
Irish Cr.
BX Cr.
Coldstream Cr.
Swan L.
Vernon Cr.
Kelowna (Mill) Cr.
Mission Cr.
Winfield
Ellison L.
Eqesis Cr.
Naswhito Cr.
Whiteman Cr.
Shorts Cr.
Lambly Cr.
Powers Cr.
Salmon River
KELOWNA
Bellevue Cr.
Chute Cr.
Robinson Cr.
Naramata Cr.
Turnbull Cr.
Penticton Cr.
Ellis Cr.
PENTICTON
Trepanier Cr.
Peachland Cr.
Peachland
Eneas Cr.
Summerland
Trout Cr.
Shingle Cr.
Shatford Cr.
Shuttleworth Cr.
Vaseux Cr.
Vaseux L.
Park Rill
Oliver
Inkaneep Cr.
Osoyoos L.
Canada
U.S.A.
B.C.
Wash.
N
Scale
5 0 5 10 15 mi
1 Kalamalka Lake
2 Okanagan Lake
3 Skaha L.
4 Vaseux L.
5 Osoyoos L.

FIG. 1. Okanagan drainage basin in Canada.

lost via evaporation. About 15% of the mean annual surface runoff to Okanagan Lake is used for irrigation.

There are three major population centers in the basin, Vernon, Kelowna, and Penticton (Fig. 1). The major industrial developments in the valley are associated with agricultural and forest industries. Current population (1971 census) in the valley is about 113,500 people.

RECENT HISTORY

Okanagan Salish Indians were the original inhabitants of the Okanagan Valley, living a nomadic existence along the shores of the lakes. There is no evidence to indicate that their presence caused environmental change to either the watershed or the lakes. White European settlers arrived around 1860, establishing large ranches to supply beef and horses to miners attracted to the Cariboo gold fields. Cattle brought from the United States through the Okanagan Valley, placed a heavy demand on native grasses. Some land clearance can be dated to this period. Early settlers obtained their livelihood by devoting acreage to forage crops. Orchardry on a large scale commenced around 1920. By 1920 the municipalities of Penticton, Kelowna, and Vernon were organized, and from 1930 to 1950 regional sewage treatment plants commenced operation, discharging their effluents to the lakes. As will be seen in later sections, these events — land clearance, overgrazing, and waste discharge — have had the greatest effects on the water quality of the main valley lakes.

Limnological Findings of Significance to Water Resource Planning

PHYSICAL LIMNOLOGY

Morphometry — The Okanagan Valley lakes represent a variety of basins, with Okanagan Lake foremost in volume, surface area, and mean depth (Table 1). Wood, Skaha, and Osoyoos lakes are much smaller, of comparable size and volume, and Kalamalka Lake is intermediate between these extremes. Vaseux Lake is the smallest of the major lakes. Maximum depth occurs in Okanagan, with Kalamalka the second deepest. Mean depth is greatest for Okanagan and least for Vaseux. There is considerable variation in theoretical water renewal rate (residence time or flushing) (Table 2). Those lakes uppermost in the chain have the longest residence times, while those receiving the outflow of Okanagan Lake (Skaha, Vaseux, Osoyoos) have much shorter average residence times (Table 2). Because of the large variation in water inflow among lakes and the large volume of Okanagan Lake, there was little relation between mean depth and residence time. For example, Wood and Osoyoos (with mean depths of 22 and 21 m, respectively) have responded quite differently to eutrophication processes because of their location in the chain (Wood at the upper, Osoyoos at the lower end) and related flushing time (Wood nearly 20 yr, Osoyoos less than 1 yr). Short residence times appear to be "protecting" the lower, shallow lakes in the series (Skaha, Vaseux, and Osoyoos) from the more serious effects of eutrophication.

The 129 "headwater" lakes in the Okanagan basin are all much smaller than the mainstem lakes on the valley floor, the largest (Swan) being only 394 ha (973 acres) in area and most under 100 ha (Table 3). All are relatively shallow, few exceeding 10 m in mean depth. Seventy-nine are impounded for agricultural storage water (Koshinsky and Andres 1972), and are subject to annual

TABLE 1. Morphometric features of six Okanagan mainstem lakes.

Lake	Volume ($10^6 m^3$)	Surface area ($10^6 m^2$)	Depths (m)		Maximum[a] length (km)	Maximum[a] width (km)	Perimeter[a] (km)
			mean	maximum			
Wood[b]	200	9.3	22	34	6.60	1.70	16.7
Kalamalka[b]	1,520	25.9	59	142	16.0	2.30	42.4
Okanagan[b]	26,200	348.0	76	242	112.8	5.22	270.0
Skaha[c]	558	20.1	26	57	11.90	2.40	29.5
Vaseux[b]	17.7	2.75	6.5	27	4.08	0.85	8.1
Osoyoos (N)[b,d]	204.0	9.91	21	63	7.55	1.75	20.4
Osoyoos (S)[b,d]	51.5	5.14	10	29	3.00	1.90	12.8
Osoyoos (Total)[e]	397.0	23.0	14	63	16.05	2.00	47.9

[a] These data were obtained from maps of the Canadian National Topographic System, 1960. Scale 1:126,720.

[b] Data compiled from charts of the Fish and Wildlife Branch, Department of Recreation and Conservation, B.C.

[c] Data compiled from a chart by A. M. Thomson, Study Director.

[d] Osoyoos (N) is the basin north of the highway bridge. Osoyoos (S) is the basin between the highway bridge and the U.S. border.

[e] Includes basin south of U.S. border.

summer drawdown usually ranging from 1 to 4 m. Theoretical flushing times vary widely between the headwater lakes, some having no surface outlet whereas others may have relatively rapid replacement, although modified considerably by storage regimes.

Thermal characteristics — In the mainstem lakes vertical and horizontal thermal structure was measured six times from spring to autumn, 1971, permitting recognition of epilimnion and thermocline depth, mean temperature, and volumes of the major layers (epilimnion, metalimnion, hypolimnion), rate of hypolimnial warming, stability, summer heat income for two lakes (Okanagan and Skaha), and internal seiche characteristics. Strong valley winds play a major role in the circulation of all major valley lakes. Some aspects of these studies have already been reported (Blanton and Ng 1972; Blanton 1972).

All the mainstem lakes are dimictic, and most have bottom water temperatures above 4 C in midsummer. Except for slightly higher mean epilimnial temperatures during midsummer in Wood Lake, all showed similar seasonal changes in that thermal characteristic (Blanton and Ng 1972), whereas mean hypolimnial temperatures were consistently different among lakes (Fig. 2). That of Wood Lake was nearly as low as Okanagan due to groundwater inflow. In at least two lakes (Wood and Skaha) late summer increases in epilimnion depth were accompanied by sharp rises in chlorophyll *a*, possibly indicating nutrient entrainment from meta- or hypolimnial sources and a stimulation of phytoplankton growth.

Headwater lakes studied (Koshinsky and Andres 1972) show sharp thermal stratification in midsummer, with mean epilimnial temperatures (14.9–22.7 C) somewhat lower than the mainstem lakes.

TABLE 2. Mean annual discharge and calculated residence time, mainstem Okanagan lakes.

Lake	Mean annual outflow[a]		Residence time
	(×10⁶*m*³)	(×10³*acre ft*)	(*yr*)
Okanagan	439.0	336.0	59.7
Skaha	474.7	385.0	1.2
Vaseux	528.8	428.9	0.03
Osoyoos (total lake Canadian and U.S. parts)	590.3	478.6	0.7
Wood	10.1	8.2	19.8
Kalamalka	21.3	17.3	71.3

[a] Data of B.C. Water Investigations Branch, August 1972.

TABLE 3. Morphometric features of 11 selected headwater lakes in the Okanagan Basin, 1971 (from Koshinsky and Andres 1972).

Lake	Elevation (*m*)	Volume ($10^6 m^3$)	Surface area ($10^6 m^2$)	Depths		Perimeter (*km* inc. islands)	Depth fluctuation (mean, 1965–71, *m*)
				mean	maximum		
Pinaus	1006	36.3	1.65	22.0	57.6	8.8	1.3
Agur	1158	.01	.003	3.3	7.0	1.2	0.6
Lambly	1158	2.8	.74	3.8	9.5	6.8	3.8
Hydraulic	1219	3.4	2.61	3.6	8.5	22.1	3.9
Headwaters	1280	3.2	.65	4.9	8.0	6.1	2.0
Jackpine	1311	1.6	.43	3.7	7.5	3.9	2.3
Oyama	1341	16.6	2.55	6.5	23.9	17.9	1.2
Swalwell	1372	29.7	3.03	9.8	30.5	16.7	2.2
Aley	1463	.33	.08	4.1	9.3	1.6	1.3
Munro	1585	.60	.14	4.3	11.3	1.5	1.4
Fish Hawk	1829	.34	.17	2.0	6.0	1.9	–

Transparency — Data on Secchi disc transparency and light transmittance at specific wavelengths were obtained for five of the mainstem lakes (Table 4). Wood and Osoyoos lakes have low transparency while Okanagan and Kalamalka are high in this respect. The ratio of blue to green transmission is low in Wood and Osoyoos but high in Okanagan and Kalamalka, suggesting that the latter pair might be more unproductive (Hutchinson 1957). Early records of water transparency in the Okanagan mainstem lakes are meager, but there is no clear evidence of a progressive decrease in clarity following eutrophication though this is suggested. None of the main lakes show any evidence of brown staining material.

Headwater lakes generally have low transparency, often with Secchi disc readings of 1–3 m, and brown humic stained water (20–65 Pt units), although a few may be more transparent (Secchi readings over 6 m) and lack staining materials (Koshinsky and Andres 1972).

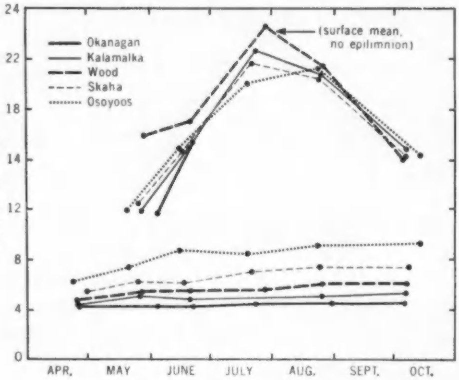


FIG. 2. Lake-wide mean temperatures of epilimnion and hypolimnion in 1971, Okanagan Basin mainstem lakes (Blanton and Ng 1972).

Current patterns — Studies on water current patterns in the Okanagan mainstem lakes were concentrated at the northern end of Skaha Lake where the Okanagan River enters, bearing nutrient rich water from Penticton's sewage treatment plant. Drogue tracking and dye diffusion techniques were used here under a range of wind stress conditions. The river current on entering Skaha Lake is deflected along its northwest end where it merges with a well defined southerly current along the west shore. This current persists in the northern half of the lake regardless of wind direction or magnitude of river flow and can even be detected in winter ice patterns. Greatest primary production was observed in this region of the lake (Stockner et al. 1972).

CHEMICAL LIMNOLOGY

Dissolved oxygen — Dissolved oxygen levels were close to saturation in epilimnial waters of all mainstem lakes throughout 1971 (Williams 1973), whereas marked differences were evident in hypolimnial oxygen content between the lakes during summer and autumn. Mean hypolimnial values rarely fell below 80% saturation in Kalamalka or Okanagan whereas in Skaha, Osoyoos, and Wood lakes, minima of 56, 27, and 6%, respectively, were observed.

The rate of summer oxygen depletion from hypolimnial water has long been used as an index of lake productivity (Hutchinson 1957), and determinations for the Okanagan mainstem lakes show some differences (Table 5). Despite the difficulties in use of such depletion rates for lakes deeper than about 75 m (Okanagan and Kalamalka) discussed by Hutchinson (1957), there seems little

TABLE 4. Water transparency and light transmission of five Okanagan mainstem lakes (from Blanton and Ng 1972).

		Percent transmission per meter				
Lake	Average Secchi disc depth, m (Apr.–Oct. 1971)	450 m filter (blue)	530 m filter (green)	630 m filter (red)	Average $\frac{(B+G+R)}{3}$	Ratio B:G
Wood	2.5	46.2	58.6	45.3	49.7	0.79
Osoyoos	3.3	56.4	67.0	56.0	56.6	0.84
Skaha	4.5	65.4	74.5	64.3	69.3	0.88
Okanagan	8.0	76.4	80.1	68.0	74.7	0.95
Kalamalka	9.0	85.6	86.0	74.5	81.8	0.99

doubt that the rate for Wood far exceeds those of other mainstem lakes, indicating high productivity, and that for Kalamalka is clearly the lowest, followed by Okanagan.

All headwater lakes selected for study showed rather severe hypolimnial oxygen depletion during summer. Their shallow depths, excessive drawdown, and large amounts of organic staining material would prevent meaningful use of hypolimnial oxygen depletion rates as an index of productivity (Hutchinson 1957), even if such data had been available.

Major ions — Although there were some differences in relative abundance of major ions among mainstem lakes (Table 6), all had Ca^{++} as the dominant cation and HCO_3^- as the dominant anion.

Concentrations of major ions in most headwater lakes were much lower than in mainstem lakes, judging from analyses reported by Koshinsky and Andres (1972), and the direct relation between total dissolved solids and elevations.

TABLE 5. Hypolimnial oxygen depletion rates for mainstem Okanagan Basin lakes, 1971.[a]

Lake	Standard depletion rate (*mg/liter⁻¹ per day*)	Areal depletion rate (*mg/cm⁻² per day*)
Wood	0.061	0.065
Osoyoos	0.035	0.038
Skaha	0.034	0.148
Okanagan	0.015	–
Kalamalka	0.009	–

[a] From Williams (1973).

Major nutrients — Concentrations of nitrogen and phosphorus present in lake water at spring overturn may be useful indicators of subsequent algal growth potential. Such determinations are available for mainstem lakes for 2 yr (Table 7). Highest nutrient concentrations for both years occur in Wood Lake, followed by Skaha and Osoyoos lakes; Okanagan and Kalamalka show the lowest spring concentrations for both nutrients. The spring nitrogen level in Wood Lake exceeds the suggested critical concentration of 300 μg liter^{-1} (Sawyer 1947; Lee 1970) on both years as does that for Skaha and Osoyoos lakes in 1970. Similarly, phosphorus levels for Wood, Osoyoos, and Skaha lakes are over the suggested critical concentrations (10–20 μg PO_4 (P) liter^{-1}) above which excessive algal blooms and aquatic plant growth may occur (Sawyer 1947; Vollenweider 1968). Wood, Skaha, and Osoyoos lakes had much lower N/P ratios compared to other mainstem lakes (Williams 1973), suggesting that nitrate rather than phosphate may be the nutrient limiting algal growth in these lakes. Loading levels to the major lakes have been calculated, and will be discussed in subsequent sections.

Some information is available on spring (1971) nutrient levels in 11 selected headwater lakes (Koshinsky and Andres 1972). Total N (Kjeldahl) in spring surface waters of the lakes ranged from a low of 130 μg liter^{-1} in Oyama Lake to a high of 1067 μg liter^{-1} in Agur Lake and showed no obvious diagnostic relations. Total phosphorus in spring surface waters ranged from a low of 30 μg liter^{-1} in Agur to a high of 180 μg liter^{-1} in Pinaus Lake. Nutrient loading has not been cal-

TABLE 6. Average concentration (Apr.–Oct., mg/liter⁻¹) of major ions in Okanagan mainstem[a] and head-water[b] lakes, 1971 (water column average).

Lake	Cations				Anions		
	Ca	Mg	Na	K	HCO_3	SO_4	Cl
Wood	28.8	17.3	19.0	4.2	177.4	30.4	2.5
Kalamalka	37.9	17.1	15.9	4.6	177.3	55.7	1.3
Okanagan	32.9	8.4	9.1	2.2	131.8	27.2	1.1
Skaha	32.8	8.4	9.5	2.1	129.9	27.6	1.4
Osoyoos	34.2	8.7	9.9	2.3	138.1	28.5	1.6
Headwater lakes[b]	1.6–21.6	0.7–18.7	1.0–29.2			1.7–17.4	

[a] From Williams (1973).
[b] Range for 11 selected headwater lakes, Koshinsky and Andres (1972).

culated or estimated for any of the headwater lakes.

TOTAL PHOSPHORUS LOAD

The total phosphorus load to each Okanagan lake was considered the most reliable indicator of current trophic state, for there was a strong relationship between the concentrations of total phosphorus in lake water at spring overturn and the amount of chlorophyll *a* in the photic zone in midsummer (Fig. 3).

Patalas and Salki (1973) using criteria based on soil- and population-dependent phosphorus export, were the first to calculate total phosphorus loads to all mainstem lakes except Ellison and Vaseux. An estimate of the actual load of nitrogen and phosphorus was obtained from measurements of nutrient concentrations in all major streams in the Okanagan drainage basin. Estimates of loads from diffuse sources came from separate studies of ground water, septic systems, and precipitation. There was good agreement between calculated and estimated loads (Patalas and Salki 1973); Stockner 1972b). These data when expressed on an areal basis and plotted as a function of mean depth divided by mean annual residence time, provide a meaningful comparison of the current trophic state of the Okanagan lakes (Vollenweider 1973) (Fig. 4).

Skaha, Osoyoos, and Vaseux currently fall within the eutrophic range but are very close to the mesotrophic position. Wood Lake, clearly the most eutrophic of the lakes, falls in the upper mesotrophic range (Patalas and Salki's calculation, however, places it in the eutrophic position). This is likely due to the difficulties encountered in measuring the phosphorus load from diffuse sources in this sub-basin. Recent estimates for 1972–73 would place it higher, closer to the figure calculated by Patalas and Salki (W. Oldham personal communication). Kalamalka falls within the oligotrophic category while Okanagan is close to the eutrophic position. These lakes are strongly influenced by long water residence times that increase the relative residence time of nutrients.

TABLE 7. Average concentrations of total nitrogen and phosphorus at spring overturn in mainstem Okanagan lakes in 1970[a] and 1971[b] (μg/liter^{-1}).

Lake	Nitrogen 1970	Nitrogen 1971	Phosphorus 1970	Phosphorus 1971
Wood	427	539	213	293
Kalamalka	264	199	14	7
Okanagan	232	189	29	31
Skaha	323	208	97	64
Osoyoos	309	235	91	62

[a] Analyses by B.C. Research Laboratory, Vancouver.
[b] Analyses by Canada Water Quality Laboratory, Calgary.

NUTRIENT SOURCES

Osoyoos Lake — The average estimated total phosphorus load to Osoyoos Lake is about 15,000 kg yr^{1-}. Over 65% of this annual load comes from the Okanagan River which drains Skaha and Vaseux lakes above, and the remainder comes from surface and subsurface agricultural return flows and from septic tanks located near the river. A small sewage treatment plant at Oliver contributes about 1800 kg yr^{1-} to Osoyoos Lake. Much of the load to Osoyoos is from uncontrollable diffuse sources and a substantial reduction in load is possible only by attitudinal or institutional change. Tertiary treatment at Penticton sewage treatment plant discharging to Skaha Lake will help reduce loads to Osoyoos.

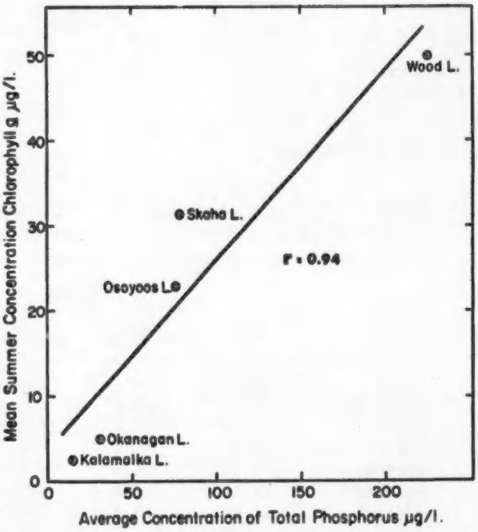


FIG. 3. Relation between chlorophyll concentration and total phosphorus content of water from the Okanagan mainstem lakes.

Vaseux Lake — The estimated total phosphorus load to Vaseux is about 9000 kg yr^{-1}. Over 90% of this load comes directly from the Okanagan River which drains Skaha Lake above. Any reduction of phosphorus load in Skaha Lake will reduce loads to Vaseux and as such represents the only feasible means of nutrient control for this lake.

Skaha Lake — The total phosphorus load to Skaha is about 22,000 kg yr^{-1}. Almost 60% of this total comes from the Penticton sewage treatment, the remainder from the Okanagan River draining Okanagan Lake, and from other surface and subsurface flows below Penticton. With the recent installation of a tertiary sewage treatment plant to remove phosphorus from the effluent (efficiencies now approaching 70–80%), the load to the lake is expected to drop substantially (Stockner 1972a).

Okanagan Lake — Average estimated annual load to Okanagan Lake is about 81,000 kg yr^{-1}. Of this total more than 45% is attributable to sewage treatment plants and industrial outfalls. The remainder comes from about 19 major streams draining a variety of land-use regions, e.g. forestry, agriculture, mining, and residential. Tertiary sewage treatment for phosphorus removal by chemical means or by land irrigation currently contemplated would improve water quality in this lake.

Kalamalka Lake — The average annual load to Kalamalka Lake is about 2000 kg yr^{-1}. No industrial or municipal outfalls enter this lake and the majority of phosphorus load is from Coldstream Creek and subsurface return flows. About 20% of the total load comes from Wood Lake which has a small inflow to the lake in the south basin. Reversal of present trends is possible only by institutional changes pertaining to land-use on the watershed, e.g. greenstrips, feedlots.

Wood Lake — Average load to Wood Lake is less than 1000 kg yr^{-1}, which seems unrealistically low in light of its current state. Recent estimates indicate that over 90% comes from septic tanks, subsurface return flow, and from Vernon Creek, draining agricultural lands. As nutrients from diffuse sources have caused and continue to amplify the current overenrichment of this lake, attitudinal or institutional changes are required before an amelioration of the eutrophic condition is seen.

GEOLIMNOLOGY

Carbon profiles — Carbon profiles for recent sediments of the Okanagan mainstem lakes show a trend toward increasing values at the surface (Fig. 5) (St. John et al. 1973). The increase noted in Okanagan, Osoyoos, and Wood lakes correlates with the period of greatest floral change on the watershed as noted by Anderson (1972). In Skaha Lake no significant increase occurred until

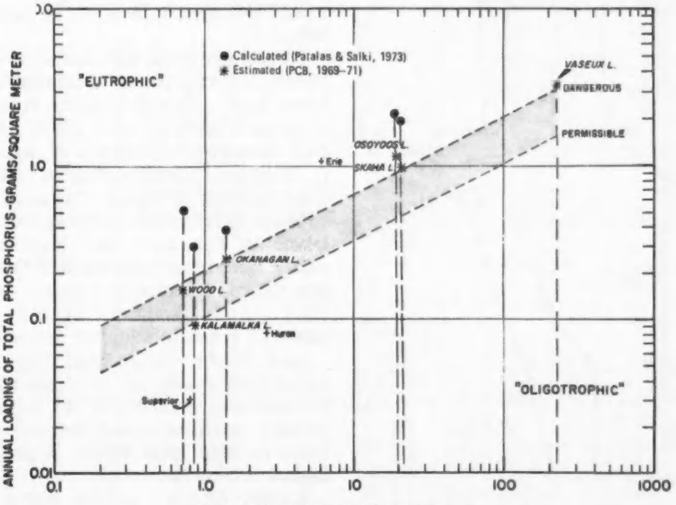


FIG. 4. Annual areal total phosphorus load to the mainstem Okanagan Basin lakes, 1969–71, (B.C. Pollution Control Branch data) and calculated (Patalas and Salki 1973).

about 25–30 yr ago (4–5 cm), when a sharp increase in carbon was apparent. This increase correlates well with the date of installation of the Penticton sewage treatment plant in 1947, and is undoubtedly attributable to this source. In Kalamalka Lake, only a minor increase in the rate of carbonate accumulation has occurred over the past decade. Other evidence given by St. John (1972) indicates that rural agricultural activities have been a primary factor in the gradual eutrophication of Wood, Osoyoos, and Okanagan lakes, although waste discharge is the chief factor in Skaha Lake.

Phosphorus — Acid extractable inorganic phosphorus content of surficial sediment was determined to estimate yearly losses of this element from the lake system (St. John 1972). Evidence indicates iron-bound phosphorus as the major form of P in the sediments with no positive correlation between absolute amounts and trophic state or concentration in overlying waters. In Skaha Lake sediments a large portion of this element is found as apatite. Much of this apatite is of terrigenous origin, but some is formed through diagenesis. This diagenetic fixation of phosphorus may assist in the reversal of eutrophication in this lake.

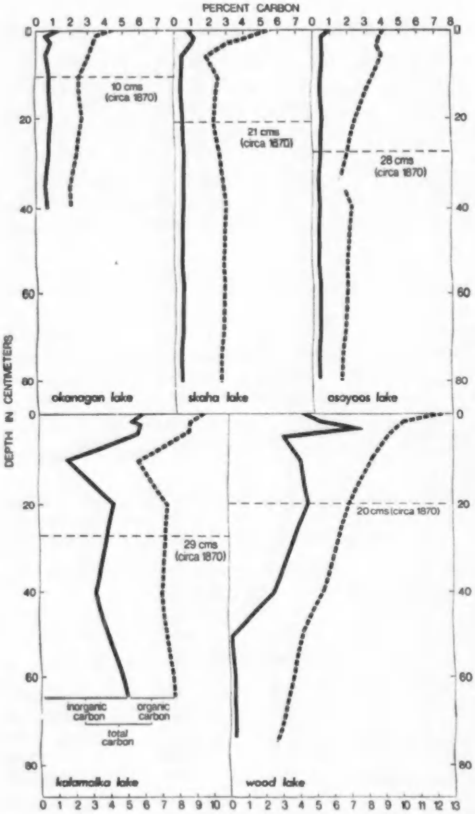


FIG. 5. Profiles of carbon content of cores from Okanagan mainstem lakes (St. John et al. 1973).

Mercury — Mercury concentrations in sediments of certain Okanagan Basin lakes appear to be enriched from as yet unidentifiable sources. Deepwater Wood Lake sediments averaged 1200 ppb Hg, with one sample as high as 2139 ppb. Average sediment values for mercury in Kalamalka were 586 ppb for the carbonate terraces, and 673 for deepwater sediment. Values in remaining lakes were between 200–600 ppb. Despite high mercury concentrates in Wood and Kalamalka lakes, concentrations in fish muscle remain low.

BIOLOGICAL LIMNOLOGY

Nutrient bioassay — To better understand the role of nutrients in regulating algal growth in the main valley lakes, laboratory studies were designed to test effects of nitrogen (NO_3) and phosphorus (PO_4) additions to natural phytoplankton populations under controlled conditions. Details of the 2-yr program are described elsewhere (Stockner et al. 1972). Typical results of a nutrient enrichment bioassay are given in Fig. 6, and summarized below.

Nitrate alone was stimulatory to algae in Wood, Skaha, Vernon Arm of Okanagan Lake, and to a lesser degree in Osoyoos Lake. It is significant that these same lakes, or areas within lakes, consistently had measurable quantities of soluble phosphorus (>10 μg liter^{-1}) and exhibited a variety of eutrophic characteristics. Thus, shortages of nitrate appear to limit algal growth in the more eutrophic Okanagan lakes. In Okanagan and Kalamalka, the most oligotrophic lakes, addition of NO_3 and PO_4 together was the most stimulatory, at all concentrations, to algal growth. Additions of NO_3 or PO_4 alone generally failed to stimulate growth.

Such results suggest that these lakes are well below their maximum production level, that both nitrogen and phosphorus are required to increase primary production, and that reduced phosphorus input to these lakes should prevent excessive biological production.

Results of pure culture bioassay experiments provided insight into which specific regions or water masses within each lake contained "residual" nutrients stimulatory to test algae (PAAP test 1969). On the basis of algal yield after 6 days from two

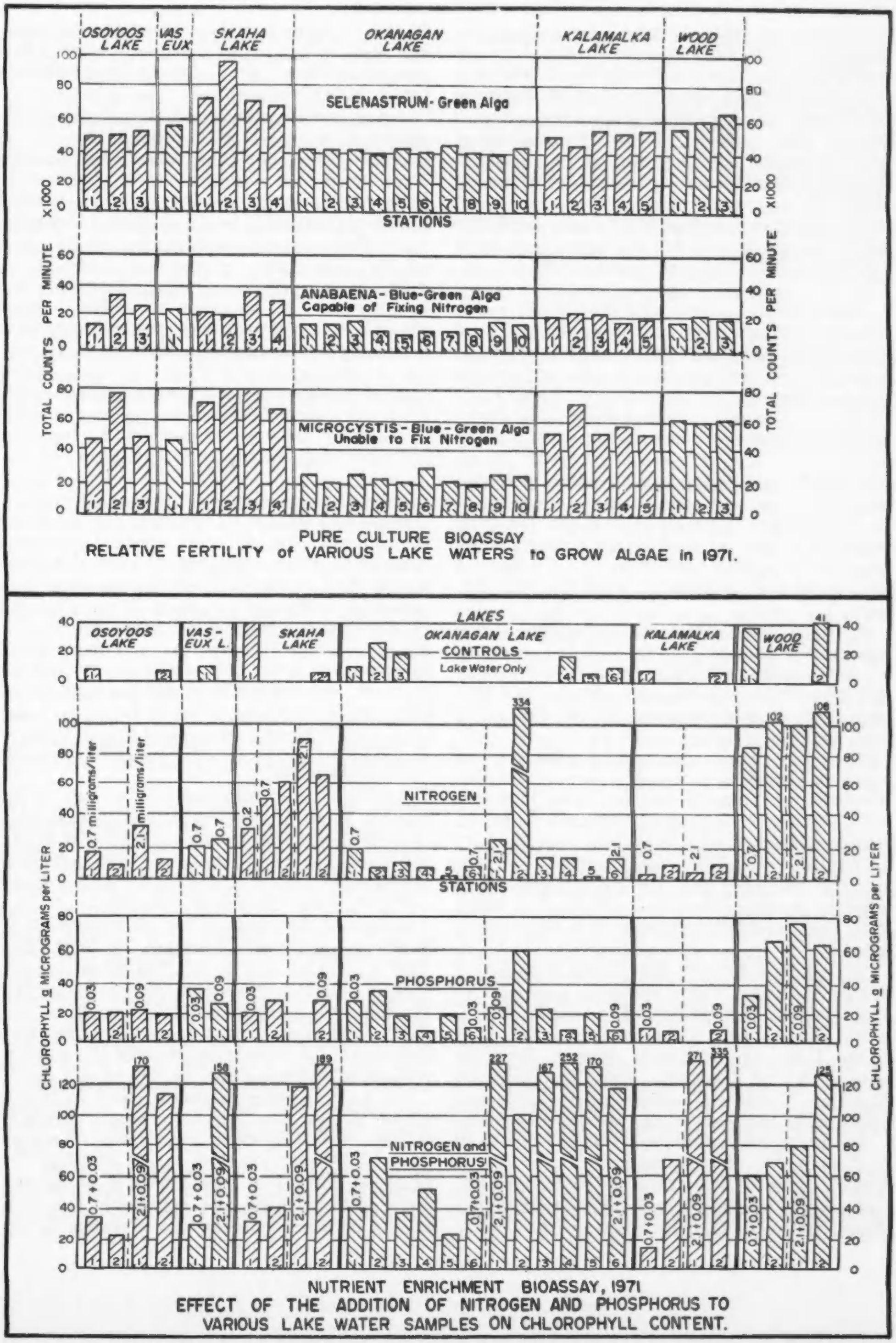


FIG. 6. Results of nutrient enrichment bioassay program 1971. (Effects of addition of nitrogen and phosphorus to lake phytoplankton. Response indicated by chlorophyll *a* content). (Station number at base of histogram).

experiments in 1971, the lakes of the Okanagan Basin could be ranked in decreasing order of nutrient availability as follows: Skaha, Wood, Osoyoos, Vaseux, Kalamalka, Okanagan lakes. On a station-to-station basis within all lakes, the most eutrophic regions were adjacent to the Okanagan River plume in Skaha and Osoyoos lakes. The most oligotrophic areas were in Kalamalka and Okanagan lakes.

No bioassays were conducted on any headwater lakes, as eutrophication is not a serious problem in any of these (Koshinsky and Andres 1972).

Phytoplankton — No detailed phytoplankton enumeration was conducted as part of the Okanagan Basin study. Stein and Coulthard (1971) included some data on phytoplankton in their report that provides the basis for following paragraphs.

The most notable feature of Wood Lake phytoplankton is the dominance of blue-green algae in most samples at all depths throughout the season. *Oscillatoria* sp. was dominant, whereas *Aphanizomenon flos-aquae* was common during the summer. A few diatoms occur in early spring but these are quickly replaced by blue-green algae. Phytoplankton population density in Wood Lake was among the highest recorded, averaging 7900 cells ml^{-1}.

Kalamalka Lake phytoplankton are sparse (<700 cells ml^{-1}). Diatoms, chiefly *Cyclotella ocellata*, *C. kutzingiana*, and *Melosira italica* were dominant. Phytoflagellates peak in early summer and fall; dominants were *Cryptomonas ovata*, *Chromulina* spp. and *Dinobryon sertularia*.

Okanagan Lake is dominated by diatoms, but there is considerable variation among stations. Densities are generally low, averaging 1500 cells ml^{-1}. Dominant diatoms in Okanagan Lake are *Melosira italica*, *Cyclotella ocellata*, and *Fragilaria crotonensis*. Blue-green algae, common in midsummer and early fall, are chiefly *Aphanotheca nidulans*, *Anabaena flos-aquae*, and *Lyngbya limnetica*. The dominant phytoflagellate is *Cryptomonas ovata*.

The phytoplankton of Skaha Lake is composed chiefly of diatoms with a blue-green algal peak in late August. Average phytoplankton density is about 3700 cells ml^{-1}. The dominant diatoms in Skaha Lake are *Asterionella formosa*, *Fragilaria crotonensis*, and *Cyclotella comta*. The dominant blue-green algae are *Aphanizomenon flos-aquae*, *Aphanothece microscopica*, and *Anabaena circinalis*.

The phytoplankton succession in Osoyoos Lake is characterized by a spring pulse of diatoms, a summer bloom of blue-greens and phytoflagellates, and a return to diatoms in the fall. The principal diatom species in Osoyoos Lake are *Asterionella formosa*, *Fragilaria crotonensis*, *Cyclotella comta*, and *Melosira italica*. The dominant phytoflagellate was *Cryptomonas ovata*. Average phytoplankton density is 5470 cells ml^{-1}.

The seasonal succession of phytoplankton provides further evidence of the trophic character of mainstem lakes. In Skaha, Wood, and Osoyoos lakes, where high concentrations of soluble phosphate occur at spring overturn, there was a rapid growth of diatoms followed by a pulse of blue-green algae, whose maximum density appeared dependent on the concentration of available phosphorus at spring overturn. In Wood Lake, where there was an abundance of phosphate at spring overturn (80 μg liter^{-1}), blue-green algae tended to dominate the phytoplankton assemblage from spring to early fall. In Okanagan and Kalamalka lakes, where concentrations at spring overturn are low (<10 μg liter^{-1}), diatoms dominate the spring pulse, with phytoflagellates common during summer, and a return to diatom dominance in the fall.

Attached algae and rooted aquatic vegetation — Over the past decade a marked increase has occurred in the abundance of rooted aquatic plants and attached microalgae (periphyton) along the shorelines of most of the main valley lakes, where high biological production is caused by the discharge of nutrients (Stockner et al. 1972). Some areas currently exhibiting extensive weed beds, where harvesting has either been carried out or has been proposed, are: Vernon Arm and Kelowna shoreline south of the floating bridge on Okanagan Lake; south end of Wood, east shore of Skaha, Vaseux, and along the west shore of Osoyoos Lake the north and middle basins.

Results of periphyton studies show that on the average, Wood Lake produced the greatest yield of periphyton of any lake (961 mg dry wt m^{-2} day^{-1}), and the Vernon Arm of Okanagan Lake the highest among stations (1200 mg dry wt m^{-2} day^{-1}) (Stockner et al. 1972). Growth of periphyton in Vaseux Lake and off the mouth of the Okanagan River in Skaha and in Osoyoos lakes was also high (800–1000 mg dry wt m^{-2} day^{-1}). The lowest average yield of periphyton was noted in Kalamalka and Okanagan lakes, averaging 200–250 mg dry wt m^{-2} day^{-1}. The average periphyton growth at other lake stations was substantially less than the above noted, with values averaging 300 mg dry wt m^{-2} day^{-1}.

The heavy periphyton growth noted in Wood, Skaha, Vaseux, and Osoyoos lakes was usually at stations located either in the vicinity of sewage effluent discharges or close to the plume of the Okanagan River. Low growth noted along the east shore of Skaha Lake was presumably due to a paucity of nutrients along this shoreline, as the main flow of the Okanagan River is directed to the western shoreline by a small training dyke. The situation noted in Skaha Lake, with one station exhibiting high and others low growth, was similar to that noted in Okanagan Lake. Low growth was noted at most stations except those adjacent to the municipal sewage outfalls at Kelowna and Vernon, where high growth occurred.

The maximum growth rate of periphyton occurred in May or early June and consisted chiefly of diatoms. A second smaller pulse dominated by green or blue-green algae occurred in late August, with a return to diatoms in fall. Results of tests of tissue concentrations of nitrogen and phosphorus in periphyton indicated that the ratio of nitrogen to phosphorus was 5:1 for periphyton growing in eutrophic waters compared to 14:1 in more oligotrophic situations (Stockner et al. 1972). Highest cellular phosphorus values were noted in samples from eutrophic locations. Nitrogen concentrations of periphyton tended to be highest in early fall in all lakes.

Periphyton communities play an important role in the nutrient balance of smaller lakes by trapping considerable quantities of nutrients as they enter. In many of the Okanagan lakes luxurious periphyton growths occur in the immediate vicinity of known nutrient discharges. Growth of attached algae in these locations, resulting from man-made nutrient inputs, could jeopardize the reproductive success of beach-spawning kokanee or other sport fish which live in the littoral zone.

Bottom fauna — After the study by Rawson in 1935 of the Okanagan lakes (Clemens et al. 1939) there was only cursory sampling of benthos in the basin lakes until the investigations of Sæther (1970) and Sæther and McLean (1972) on the mainstem lakes, and of Koshinsky and Andres (1972) who sampled 11 of the headwater lakes.

The benthos of Wood Lake in 1971 had changed markedly from that reported by Rawson 36 yr earlier (Sæther and McLean 1972) when the fauna was characteristic of a normal eutrophic lake with a dense population of oligochaetes and chironomids, but now both these groups appear in sharply reduced numbers at most depths. Although bottom waters of Wood Lake are subject to a long and severe seasonal depletion of oxygen, this does not seem a reasonable explanation for the reduced abundance of benthos. Sæther and McLean suggested the possibilities of toxic pollutants in the sediments, but whatever the cause, they maintain that the change in abundance and composition of benthos indicates a further progression in eutrophication of the basin rather than the reverse.

Although no dramatic change has occurred in the abundance of benthic organisms in Kalamalka Lake between 1935 and 1971, Sæther and McLean did find an apparent decrease in the relative abundance of chironomids (about 95% in 1935, 55% in 1971).

Skaha Lake shows evidence of a recent and dramatic change in composition of its benthos (Sæther 1970). Chironomids other than *Procladius* are absent from the deeper stations and deformed chironomids were found at several locations. Both chironomids and oligochaetes were evident in several benthic samples taken at depths of 10 m or less from Vaseux Lake, whereas only oligochaetes were found in those from a deep (22.5 m) station where dissolved oxygen was severely depleted (August 1967 data, B.C. Fish and Wildlife Branch). The benthos composition of Osoyoos Lake would categorize its northern basin as moderately eutrophic and its central basin as strongly eutrophic (Sæther 1970).

On the basis of his studies on the benthos of mainstem lakes, Sæther identified Wood as most eutrophic, followed by Osoyoos and Skaha, but Kalamalka and Okanagan were essentially oligotrophic.

The bottom fauna of 11 selected headwater lakes was sampled to determine its quantity and composition (Koshinsky and Andres 1972). Abundance ranged from a low of 246 organisms m^{-2} (Headwaters Lake No. 1) to a high of 2550 (Oyama Lake), none reaching the densities recorded for Skaha (3892–9935 m^{-2}) or Osoyoos (5500 m^{-2}) in recent years. Many, but by no means all, of the lakes subject to severe summer drawdown, showed very low benthic biomass, as did most of those at higher altitudes.

Zooplankton — Changes in the crustacean plankton in relation to eutrophication of most Okanagan mainstem lakes have been described by Patalas and Salki (1973); only major points will be presented here. There has been no substantial change in species composition of the crustacean plankton of either Kalamalka or Okanagan lakes since 1935, although abundance (average volume of settled plankton; mm^3 cm^{-2}) in Okanagan has apparently increased by 3 to 5 times (Table 9). Plankton abundance in Skaha Lake in 1948 was similar to 1935 levels in Kalamalka and Okanagan, but in recent years has been over 6 times that previously recorded. No significant differences in zooplankton composition and structure were found between Skaha and Okanagan or between Skaha and Osoyoos lakes. Only 6 species of crustacean plankters were found in recent Wood Lake samples, compared to

9 in Kalamalka, 13 in Okanagan, 12 in Skaha, and 11 in Osoyoos. Numerically the abundance of Wood Lake crustacean plankters was higher than all mainstem lakes except Skaha, and volumetrically far above all, although this was in part a result of the considerable amount of phytoplankton which could not readily be separated from samples.

Numerical abundance of crustacean zooplankton in 11 headwater lakes (Koshinsky and Andres 1972) ranged from a low of 26 individuals cm^{-2} in Alex Lake to a high of 246 cm^{-2} in Pinaus Lake. Seven had abundances below 100 cm^{-2}, considerably lower than in most mainstem lakes.

Fish — Fish of the mainstem lakes were utilized as indices of eutrophication by making comparisons of certain of their attributes among lakes at the present time, as well as over several decades within particular lakes. Characteristics of fishes which may reflect effects of eutrophication or more general pollution include the relative abundance of species, their size (length–frequency and length–weight relations), their growth rate, and their load of trace metals, pesticides, or other contaminants.

During the 1971 spring, summer, and autumn sampling program, 26 different types of fish were taken from the mainstem lakes (Northcote et al. 1972). Only 10 of these occurred in Wood Lake, whereas 14 were recorded from Kalamalka, 15 from Okanagan, Skaha, and Vaseux, and 20 from Osoyoos. Standard gillnet catches of all fish were lowest in Wood, followed by Kalamalka. Those from Okanagan were intermediate, with much higher catches being taken from Skaha and by far the most from Vaseux. The contribution of salmonoids to the total catch was lowest in Wood (12%), followed by Vaseux (19%), Skaha (about 35%), and Osoyoos (about 40%). Catches of salmonoids at the various stations in Okanagan and Kalamalka lakes in nearly all cases were well over 40%, some ranging as high as 70%.

Several species of fish in Wood and Kalamalka averaged the smallest in length of all mainstem lakes; these included kokanee, largescale suckers, peamouth chub, and squawfish. On the other hand, Skaha Lake had the largest kokanee and lake whitefish. A similar trend was evident in the length–weight relation of the fish, those from Wood and Kalamalka generally showing the lowest regression slopes, whereas those from Skaha usually had the highest. Too few salmonoids (the only species aged) were obtained from Wood to permit reliable growth rate determinations, but those for Kalamalka salmonoids generally were lowest and those for Skaha again highest.

High concentrations of total DDT (up to 50 ppm) were found in large rainbow trout and mountain whitefish from Kalamalka Lake as well as in rainbow trout from Okanagan Lake (Northcote et al. 1972); most other species examined from the mainstem lakes had relatively low concentrations of this pesticide in their muscle tissue. High concentrations of mercury (0.5–1.8 ppm) were detected in some rainbow trout and squawfish from Okanagan, Skaha, and Osoyoos; most other species examined from the mainstem lakes contained relatively low amounts of trace metals.

Evidence of eutrophication in the mainstem lakes also can be seen by comparing fish statistics taken several decades ago with the recent analyses. Data from 1935 on Wood and Okanagan provide the longest time interval for comparison. Catches in net sets from Wood Lake were much larger in 1935 than in 1971. Furthermore, the relative abundance

TABLE 8. Late summer abundance of crustacean plankton in Okanagan Basin mainstem lakes.

Lake	1935[a] volume[d]	1948[e] volume	1969[b] numbers[c]	1969[b] volume	1971[b] numbers[c]	1971[b] volume
Wood	15.4				139	31.1
Kalamalka	4.5				136	10.9
Okanagan	2.8		188	13.3	102	7.8
Skaha		3.8	238	23.2	236	24.1
Osoyoos			161	25.9	76	10.9

[a] From Rawson's data (Clemens et al. 1939).

[b] From Patalas and Salki (1973).

[c] Individuals cm^{-2}.

[d] Settled volume (mm^3 cm^{-2}).

[e] Ferguson (1949).

of carp seems to have increased considerably in the open waters of this lake. No marked change has occurred in abundance of Okanagan Lake fish as indicated by net sampling, although again carp were taken much more frequently there in 1971. Total catches from Skaha Lake were somewhat higher in 1948 than 1971, whereas the relative contribution of salmonoids in the catch fell sharply over that period (from about 15% to less than 5%). The average length of kokanee, lake whitefish, largescale sucker, and squawfish all increased in Skaha Lake between 1948 and 1971, the first two species strikingly so. Similar changes were evident in the length-weight relations and growth rates of these and other Skaha fishes between these years. In contrast, there has been no significant change in the length–weight regression of Okanagan rainbow trout between 1935 and 1971, or in their growth rate up to the third year (thereafter it appears considerably slower in 1971 samples).

Virtually all headwater lakes in the Okanagan basin (126 of 129) support rainbow trout populations most of which originated from, or are maintained by, annual hatchery introductions. Brook trout, yellow perch, bass, longnose suckers, and dace are found in a few lakes, but the major sport species is rainbow trout. Gillnet catches of trout were lowest in lakes subject to severe water level manipulation, particularly where this was combined with competing species of fish (Koshinsky and Andres 1972). Growth rate of rainbow trout in the headwater lakes was in general much slower than in mainstem lakes, and was inversely related to altitude of the lakes, extent of drawdown, presence of competitor fishes, and opportunity for natural reproduction. Muscle tissue of rainbow trout from seven of the headwater lakes was analyzed for pesticides (DDT and derivatives) as well as trace metals (Koshinsky and Andres 1972). All concentrations detected were well below accepted tolerance levels, in contrast to amounts found in large trout from Kalamalka and Okanagan lakes.

Paleolimnology — The primary objective of paleolimnological studies was to provide a baseline of long-term lake conditions and to separate any changes from the effects of more recent man-induced disturbances, i.e. mining, logging, and sewage disposal systems.

Effects of over-grazing and land clearance on native flora are seen in pollen diagrams for Osoyoos Lake (Fig. 7), illustrating the general trend evident in nearly all the main lakes (Anderson 1972). Total pollen is relatively high at the base of the diagram, but declines to minimum values near 23 cm; that of spruce, pine, hemlock, and grass all decline sharply around 28 cm, with increases seen in the distribution of poplar, alder, willow, and sagebrush pollen. The most recent peak of poplar, alder, and weedy herbaceous plant pollen is a result of their dispersion onto newly disturbed and burned-over areas. It is speculated that by 1950 stabilization had occurred on the benchlands, and the higher pollen numbers in the surface sediment may signify a trend toward better land management. Carbon profiles also reflect these watershed changes (Fig. 5).

Diatom microfossil enumeration revealed a striking similarity in past diatom floras among lakes. In the most recent sediments (0–25 cm), noticeable differences in diatom plankton occurred as a result of man-induced disturbance. Lakes most strongly exhibiting these changes are Wood and Skaha; the former exhibited a striking increase in total diatom plankton, concomitant with the first record of stream diversion and intensive agriculture on the Wood Lake watershed some 40–50 yr ago. This

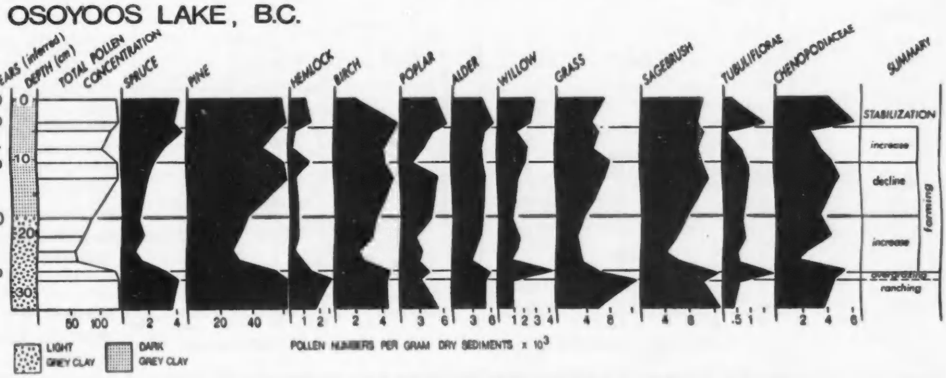


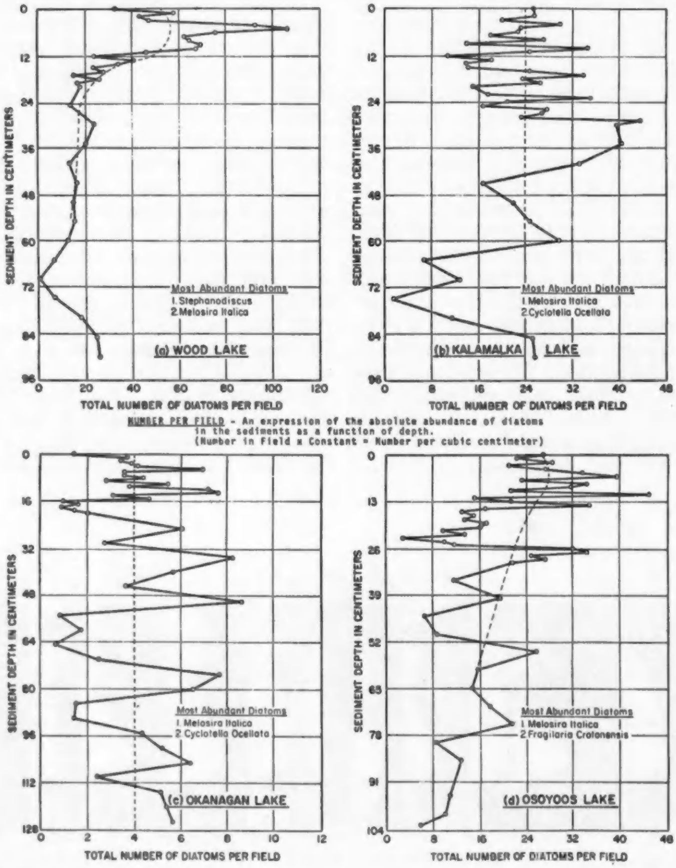
FIG. 7. Sediment pollen profiles, Osoyoos Lake, British Columbia (Anderson 1972).

factor undoubtedly altered water residence time, and increased the relative residence time of nutrients. *Stephanodiscus hantschii* in Wood Lake exhibits a large population increase commensurate with alterations of flow.

In Skaha Lake, *Fragilaria crotonensis* increased significantly following discharge of treated wastes from Penticton, while *Melosira italica* decreased (Stockner 1972b). The diatom floras of Okanagan and Kalamalka lakes exhibited some degree of trophic equilibrium throughout the column examined and appear, from the microfossil record, to have changed only slightly over the past 100 yr.

Total diatom microfossil number, which is a reflection of past lake diatom production, is significantly higher in the most eutrophic lakes, Wood and Osoyoos (Fig. 8); Skaha is not shown but diatom density is between that in Okanagan and Osoyoos (Stockner 1972b). Diatom numbers in Kalamalka were high when compared with Okanagan, considering their general trophic similarities. Okanagan showed the lowest density of diatoms in recent sediment.

The diatom analysis of Wood is most revealing in terms of understanding the eutrophication of this lake. The rapid increase in diatom numbers reflects a short period of near optimal conditions. The decline in numbers in most recent sediment is an indication of the dominance of blue-green algae in the plankton over the past few decades, at the expense of continued diatom growth. Rawson in August 1935 noted the low transparency in Wood



NUMBER PER FIELD - An expression of the absolute abundance of diatoms in the sediments as a function of depth. (Number in Field x Constant = Number per cubic centimeter)

FIG. 8. Abundance of diatoms in lake sediment as a function of depth for Wood, Kalamalka, Okanagan, and Osoyoos lakes.

(<1 m) due to a bloom of *Aphanizomenon flos-aquae*. It is likely therefore that at this time diatoms had already begun to decline in relative importance in Wood Lake.

Trophic Condition

The categorization of lakes on the basis of biological production (lake typology) has had a long and complicated history with the evolution of terms to describe various lake stages equally as complex as the actual assessment of trophic state (Hutchinson 1969). One of the more logical systems includes concepts of lake productivity that consider conditions of production (nutrient supply) and some of the effects (Rodhe 1969b). Some of the variables thought to be useful in expressing the relative trophic position of mainstem Okanagan lakes are summarized in Table 9.

Wood Lake stands out as the most eutrophic lake in the Basin. Nutrient availability, chlorophyll *a*, phytoplankton, and periphyton crop are but a few of the more notable diagnostic variables indicating this condition. Excessive primary production over several decades has led to an appreciable oxygen deficit. This factor together with deterioration of spawning habitat have seriously stressed the salmonoid fish populations in the lake. The long water renewal rate has led to nutrient recycling and coupled with anaerobic conditions in bottom waters enhanced nutrient feedback from the sediments.

Kalamalka has the longest water renewal rate of any mainstem lake, but lack of watershed development has reduced nutrient input and maintained oligotrophic conditions. Variables best depicting this condition are nutrient availability, chlorophyll *a*, periphyton, phytoplankton biomass, and percentage of salmonoid fishes (Table 9).

Okanagan with its immense volume has maintained its basic oligotrophic characteristics despite significant watershed disturbance. Certain regions exhibit eutrophic features (Vernon Arm and Kelowna foreshore) but these remain localized and have not appreciably affected the main body of the lake. There are some signs of change, especially in zooplankton biomass (4 × the 1935 estimate) and zoobenthos species composition. Salmonoids still predominate and O_2 values in the hypolimnion have not changed appreciably from the 1935 condition.

TABLE 9. Summary of parameters of use in assessing trophic state.

Variable	Osoyoos	Vaseux	Skaha	Okanagan	Kalamalka	Wood
Position in chain	6	5	4	3	2	1
Water renewal (yr)	0.7	0.03	1.2	59.7	71.3	19.8
$\bar{x}$ annual Secchi (m)	3.3	–	4.5	8.0	9.0	2.5
O_2 deficit (mg liter^{-1} day^{-1})	0.035	–	0.34	0.015	0.009	0.061
PO_4, NO_3 spring nutrient conc. $\bar{x}$(μg liter^{-1})	15(P), 16(N)	–	15(P), 10(N)	2(P), 20(N)	4(P), 23(N)	83(P), 26(N)
Limiting nutrients	NO_3	PO_4, NO_3	NO_3	PO_4, NO_3	PO_4, NO_3	NO_3
$\bar{x}$ chlorophyll *a* (μg liter^{-1})	23	–	31	5	2.5	50
Tot. phosphorus load kg/yr^{-1}	21,950	8680	21,860	188,500	2625	4650
Phytoplankton avg no. cells liter^{-1})	5475	–	3747	1800	400	7900
Periphyton growth avg (mg m^{-2} day^{-1})	258	517	231	225	124	481
Zooplankton vol (mm^3 cm^{-2})	15–20	–	20–25	10–15	10–15	20
Benthos (no. m^{-2})	5502	–	6913	2178	1087	753
Coarse fish/salmonoids	1.38	4.0	2.03	1.04	1.08	7.3
% salmonoids in total catch	42	20	33	49	49	12
Population in drainage basin	3000	–	20,000	60,000	4000	2000
Area drainage basin (10^2 m^2)	1269	–	829	6061	192	55
Trophic state	Mesoeutrophic	Mesotrophic	Mesoeutrophic	Oligotrophic	Oligotrophic	Eutrophic

It is difficult to assess the trophic condition of Skaha solely on the basis of variables presented in Table 9. Some, such as chlorophyll *a* and nutrient availability, point to the eutrophic state while others (periphyton, Secchi) do not. The short water renewal rate has undoubtedly prevented the rapid deterioration of surface water quality and has perpetuated, especially along the eastern shoreline, oligotrophic features. A decline in percentage of salmonoids over the past 20 yr together with the largest average density of benthos are but a few of the more notable signs of change commensurate with sewage discharge beginning in 1947.

Vaseux is little more than an enlargement of the Okanagan River. Its extremely short water renewal rate has protected it from excessive biological production resulting from the export of nutrients from Skaha as it has undergone change over the past 25 yr. Next to Wood it has the lowest percentage of salmonoids, but this is more likely related to lack of suitable habitat than to trophic condition.

Osoyoos exhibits in most variables an intermediate position between Wood and Okanagan lakes. Its short water renewal rate has, like Skaha and Vaseux above it, protected it from the effects of excessive biological production. Next to Wood it exhibits the highest stock of phytoplankton and the lowest mean annual Secchi reading.

The relative position in the chain has been a more critical feature to Skaha, Vaseux, and Osoyoos than their respective nutrient supplies. Wood, Skaha, and Osoyoos have similar mean depths but the annual phosphorus load to Skaha and Osoyoos is 3–5 times greater than to Wood, yet Skaha and Osoyoos exhibit less eutrophic features than Wood. Clearly, water residence time is a very important consideration in the overall assessment of current biological state or the nutrient assimilative capacity of lakes.

Contribution of Limnology to Development of the Comprehensive Plan

The ultimate role of comprehensive planning is to manage the water resource for social betterment and an optimal balanced economy, without jeopardizing environmental quality. It must be kept in mind, therefore, that the following critique is a review of limnological contributions from a management and not a scientific viewpoint. In this parti-

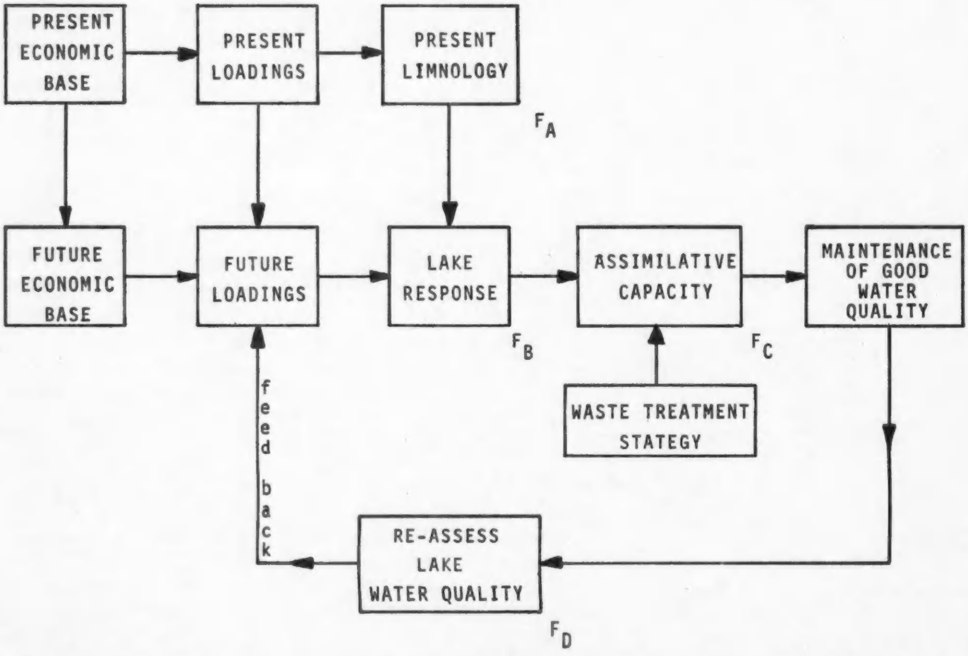


FIG. 9. Flow diagram depicting major functions fulfilled by limnology program in comprehensive water resource planning.

TABLE 10. Major limnology studies, their contribution, basic and supportive components, and linkage with other studies in development of the comprehensive plan.

	Studies	Contribution	Linkage	Basic components	Supportive components
(1)	Geolimnology	History of lake change, sediment chemistry, bathymetry	Paleolimnology, chemical, physical studies	Carbon profiles, phosphorus deposition, mercury content of sediments	Sediment particle size, detailed geochemistry
(2)	Paleolimnology	History of lake change, diatom species compositional change, watershed change (pollen analysis)	Geolimnology, phytoplankton studies, land-use surveys	Diatom and pollen studies	–
(3)	Chemical limnology	Nutrient content, O_2 deficits, major ions, knowledge of existing state	Bioassay studies, fisheries management	Nutrients, major ions, oxygen	–
(4)	Physical limnology	Temperature structure, light and transparency, currents in Skaha Lake, morphometry, knowledge of existing state	Determination of assimilative capacity, residence time (flushing)	Transparency, morphometry, temperature structure	Currents in Skaha, heat budget, circulations
(5)	Bioassay	Indication of element(s) regulating algal growth, knowledge of existing state	Ranking of trophic state of lakes, waste treatment studies	Nutrient enrichment experiments, pure culture work	Boron and trace metal studies
(6)	Phytoplankton	Knowledge of existing state, chlorophyll *a* content	Chemistry, bioassay, zooplankton, recreation studies, ranking of lake trophic state	Chlorophyll *a*, species composition	–
(7)	Periphyton	Knowledge of existing state, weed harvesting methods	Recreation studies, lake trophic state, identification of diffuse loading sources, fisheries	Periphyton growth, littoral mapping	N and P content in tissue
(8)	Zooplankton	Knowledge of existing state, history of lake change, trophic state	Paleolimnology, fisheries management	Zooplankton biomass, loadings	Oxygen, nutrients
(9)	Benthos	Knowledge of existing state	Geolimnology, chemistry	Biomass, species composition	Detailed taxonomic considerations
(10)	Fish populations	Knowledge of existing state, heavy metal and pesticide content	Fisheries management, zooplankton, chemistry	Species composition, density, comparison with previous fish work	–
(11)	Headwater lake limnology/fisheries	Knowledge of existing state of headwater lakes, effects of drawdown, heavy metal and pesticide content	Fisheries management, stream water quality	Minimum study for diagnostic characteristics	–

cular planning study the major contribution of limnological knowledge was to the water quality and waste treatment programs, that were responsible for maintaining or improving water quality via the development of waste treatment or land-management alternatives. In this capacity, limnological research served four basic functions:

F_A	To provide an assessment of current conditions.
F_B	To predict lake response for future waste loadings.
F_C	From B above, to estimate lake assimilative capacity.
F_D	To develop a monitoring program to assess lake response to implementation of waste management plans.

The manner and sequence in which these functions were married to the development of overall planning strategies is diagrammatically illustrated in Fig. 9.

To expedite evaluation of these contributions to various programs, we have attempted to identify their main contributions and possible linkages with other studies (Table 10). This information enables a comparison to be made between specific studies and their overall function (role) in development of the comprehensive plan (Table 11).

Essentially all limnological studies were necessary to an understanding of current conditions, thereby contributing directly to Function A. Fewer were of direct use when predicting lake response to future loads (Function B). Fewer still contributed to Function C — determination of lake nutrient assimilative capacity. Only five studies served to guide future lake monitoring. One way to judge the effectiveness of a particular study is to determine the number of functions it fulfilled (Table 11). It is worthwhile to identify those studies or components of studies considered to be of most direct use in this study.

TABLE 11. Matrix depicting function(s) fulfilled by major limnological studies. Study numbers are those given in Table 10.

Functions	Studies
A	1 2 3 4 5 6 7 8 9 10 11
B	*2 5 6 7 10*
C	1 2 3 4
D	3[a] 4[a] 5[a] 7[a] 8
Studies and number of contributions to functions ( ).	1(2), 2(3), 3(3), 4(3), 5(3), 6(2), 7(3), 8(2), 9(1), 10(2), 11(1)

[a]Certain parts only.

Five studies were major contributors: Paleolimnology, chemical and physical limnology, bioassay, and periphyton. Remaining investigations contributed more to specific programs than to general functions. The headwater lakes limnology program, though included in this matrix, perhaps should be removed as it fulfils all four functions in terms of its contribution to headwater lake management, but does not contribute directly to mainstem water management.

There were certain components of some studies which yielded little direct information to development of the overall plan. Some of these are identified in the supportive components column of Table 10. These studies in most cases did not solve basic management oriented problems, but they did lead to the discovery of unexpected processes operative in the lakes. For example, the heat budget calculated for Wood Lake confirmed suspicions of a possible influx of cold ground water to the hypolimnion, and the sediment studies in Kalamalka Lake led to the discovery of the active precipitation of $CaCO_3$ from the epilimnion and hence to a better understanding of the carbonate cycle in this lake. Similarly, without geochemical sediment studies we would have been completely unaware of the potential mercury problem in the Okanagan Basin.

If budgetary constraints had not been imposed at the outset, many extraneous studies would have been included in the limnology program. Paring down of expansive programs to "bare bones" limnology has proved to be a valuable feature of the initial planning procedure and should be encouraged in future studies of this type. In any long-term study where unexpected findings may require program redirection, budgetary flexibility is essential. Unfortunately, the limnology program of the Okanagan Basin studies was locked into a fixed yearly budget which did not allow for the expansion of certain studies, desirable as preliminary findings emerged.

There were some factors worthy of mention pertaining to cooperation between groups involved in large interjurisdictional studies. The limnologist's advice should be sought when establishing monitoring stations for estimates of nutrient load. In this particular study more meaningful information on nutrient load could have been gained by better communication. In future studies where water quality problems require an appreciation of nutrient source and supplies, it may only be necessary to estimate nutrient loading using Vollenweider's criteria (Patalas and Salki 1973) instead of committing considerable sums of money, and delegating man-years to direct measurement. The similarity of calculated and estimated loads in this study has already been mentioned, and this, together with the findings of Patalas (1973), lends credence to a more simplified approach.

One cannot conclude a report of this nature without a strong endorsement of the comprehensive planning approach to water resource management. Clearly, without the support of economists, hydrologists, sanitary engineers, planners, and sociologists, to mention but a few of the many disciplines involved, limnologists could not and would not have played an effective role. Limnologists should not be afraid to participate in these endeavors for fear of losing the scientific merit of their work in the shuffle of direct application to real problems. Without their contribution the depth of our understanding of the water resource would be lost.

Acknowledgments

Much of the information presented in this paper comes from reports submitted to the Okanagan Basin Study Committee. Appropriate credit is given in text, figures, and tables to these authors, but we wish here formally to acknowledge their contribution and extend our appreciation for the use of these data, much of which is unpublished. Special thanks are extended to Drs J. O'Riordan and B. St. John for fruitful discussions on the comprehensive planning process. The assistance of Mr A. M. Thomson, Study Director, and his staff in Penticton, B.C., is most gratefully acknowledged.

ANDERSON, T. W. 1972. Historical evidence of land use in a pollen profile from Osoyoos Lake, British Columbia. Geol. Surv. Can. Rep. Activ. Pap. 7: 178–180.

BLANTON, J. O. 1972. The circulation of effluent from the Okanagan River as it enters Skaha Lake. Okanagan Basin Study Committee Prelim. Rep. No. 19: 14 p.

BLANTON, J. O., AND H. Y. F. NG. 1972. The physical limnology of the mainstem lakes in the Okanagan basin, British Columbia. Okanagan Basin Study Committee Prelim. Rep. No. 20: 34 p.

CLEMENS, W. A., D. S. RAWSON, AND J. L. MCHUGH. 1939. A biological survey of Okanagan Lake, British Columbia. Bull. Fish. Res. Board Can. 56: 70 p.

COULTHARD, T. L., AND J. R. STEIN. 1969. Water quality deterioration in Osoyoos Lake, British Columbia. B. C. Water Resour. Serv. Water Invest. Branch. (unpublished report)

FERGUSON, R. G. 1949. The interrelations among the fish populations of Skaha Lake, B.C. and their significance in the production of Kamloops trout (*Salmo gairdnerii kamloops* Jordan). Univ. British Columbia, Vancouver, B.C. 84 p. (undergraduate paper)

HUTCHINSON, G. E. 1957. A treatise on limnology. Vol. 1. Geography, physics and chemistry. John Wiley and Sons, New York, N.Y. 1015 p.

1969. Eutrophication, past and present, p. 17–26. *In* Eutrophication: causes, consequences, and correctives. National Academy of Sciences, Washington, D.C.

KOSHINSKY, G. D., AND J. E. ANDRES. 1972. The limnology — fisheries of headwater lakes in the Okanagan basin. Okanagan Basin Study Committee Prelim. Rep. No. 14: 144 p.

LEE, G. F. 1970. Eutrophication. Univ. Wisconsin Water Resour. Cent. Occas. Pap. No. 2: 39 p.

NASMITH, H. 1962. Late glacial history and surficial deposits of the Okanagan Valley, British Columbia: B.C. Dep. Mines Petrol. Resour. Bull. 46: 46 p.

NORTHCOTE, T. G., T. G. HALSEY, AND S. J. MACDONALD. 1972. Fish as indicators of water quality in the Okanagan Basin lakes, British Columbia. Okanagan Basin Study Committee Prelim. Rep. No. 22: 79 p.

PAAP. 1969. Provisional algal assay procedure. Joint Industry/ Government Task Force on Eutrophication. New York, N.Y. 62 p.

PATALAS K. 1973. The eutrophication of lakes in the Okanagan Valley, British Columbia, p. 336–346. *In* Symp. on the Lakes of Western Canada, Edmonton, Alberta.

PATALAS K., AND A. SALKI. 1973. Crustacean plankton and the eutrophication of lakes in the Okanagan Valley, British Columbia. J. Fish. Res. Board Can. 30: 519–542.

RODHE, W. 1969a. Limnology, social welfare, and Lake Kinneret. Verh. Int. Verein. Limnol. 11: 40–48.

1969b. Crystallization of eutrophication concepts in Northern Europe, p. 50–64. *In* Eutrophication: causes, consequences and correctives. National Academy of Sciences, Washington, D.C.

SAETHER, O. A. 1970. A survey of the bottom fauna in lakes of the Okanagan Valley, British Columbia. Fish. Res. Board Can. Tech. Rep. 196: 1–26.

SAETHER, O. A., AND M. P. MCLEAN. 1972. A survey of the bottom fauna in Wood, Kalamalka and Skaha lakes in the Okanagan Valley, British Columbia. Okanagan Basin Study Committee MS. 26 p.

SAWYER, C. N. 1947. Fertilization of lakes by agricultural and urban drainage. Sewage Ind. Wastes 24: 768–776.

STEIN, J. R., AND T. L. COULTHARD. 1971. Water quality deterioration in Osoyoos Lake, British Columbia. B.C. Water Resour. Serv. Water Invest. Branch. 000 p. (unpublished report)

ST. JOHN, B. E. 1972. The limnology of the Okanagan mainstem lakes. Okanagan Basin Study Committee Prelim. Rep. No. 18: 41 p.

ST. JOHN, B. E., SLY, AND R. I. THOMAS. 1973. The importance of sediment studies in western lakes as a key to basin management, 145–174. *In* Symp. on the Lakes of Western Canada, Edmonton, Alberta.

STOCKNER, J. G. 1972b. Nutrient loadings and lake management alternatives. Okanagan Basin Study Committee MS. 14 p.

1972d. Diatom succession in the recent sediments of Skaha Lake, British Columbia. Okanagan Basin Study Committee Prelim. Rep. No. 12: 18 p.

STOCKNER, J. G., G. R. GIRMAN, AND R. ROBARTS. 1972c. Algal nutrient addition and pure culture bioassay on six lakes in the Okanagan Basin, British Columbia. Okanagan Basin Study Committee Prelim. Rep. No. 11: 63 p.

STOCKNER, J. G., M. POMEROY, W. CARNEY, AND D. FINDLAY. 1972a. Studies of periphyton in lakes of the Okanagan Valley, British Columbia. Okanagan Basin Study Committee Prelim. Rep. No. 33: 23 p.

VOLLENWEIDER, R. A. 1968. The scientific basis of lake and stream eutrophication, with particular reference to phosphorus and nitrogen as eutrophication factors. Organ. Econ. Coop. Dev. (Paris) Tech. Rep. DAS/CSI/68.27: 182 p.

1973. Input-output models. (In preparation)

WILLIAMS, D. J. 1973. General limnology of the Okanagan mainstem lakes. Okanagan Basin Study Committee Prelim. Rep. No. 19: 14 p.

A Review of Research on the Limnology of West Blue Lake, Manitoba[1]

F. J. Ward

Department of Zoology
University of Manitoba, Winnipeg, Man. R3T 2N2

and G. G. C. Robinson

Department of Botany
University of Manitoba, Winnipeg, Man. R3T 2N2

Ward, F. J., and G. G. C. Robinson. 1974. A review of research on the limnology of West Blue Lake, Manitoba. J. Fish. Res. Board Can. 31: 977–1005.

An interdisciplinary research program on the West Blue Lake ecosystem is reviewed. The composition, seasonal occurrence, abundance, and primary productivity of the phytoplankton are reported. In spring "net" phytoplankton diversity and abundance were highest with diatoms predominating. In summer *Anabaena spiroides* and *Aphanizomenon flos aquae* were a major component. During winter both cell numbers and species diversity declined. *Cyclotella bodanica* became dominant. Average summer phytoplankton primary productivity approximated 320 mg C m^{-2} day^{-1} in both 1971 and 1972. Average daily estimates (exclusive of zooplankton) of organic carbon in the euphotic zone during summer periods in 1971 and 1972 were, respectively, 5 and 8 g C m^{-2}.

Kinetic parameters for the bacterial uptake of 11 dissolved organic substrates are reported. Values V_{max} ranged from 0.003 mg C m^{-3} h^{-1} for formic acid to 0.115 mg C m^{-3} h^{-1} for lactic acid; turnover times from 8 h for malic acid to 950 h for glycolic acid, and (Km + S) values from 0.288 mg C m^{-3} for malic acid to 47.883 mg C m^{-3} for glucose. A relation between V_{max} values and plated bacterial counts is described for six organic acids. Evidence for proliferation and adaptation of bacteria in sample bottles is presented and the absence of photoheterotrophy described. Potential bacterial production during the summer of 1972 ranged from 18.24 mg C m^{-2} day^{-1} to 67.44 mg C m^{-2} day^{-1}. The relationship between this production and temperature ($Q_{10} = 3.129$) is described. "Filtration effect," as a source of error, in measuring glucose uptake is probably an artifact.

Generally, *Cyclops bicuspidatus* was more abundant than *Diaptomus siciloides*. Both were relatively scarce in summer. *Daphnia pulicaria* were usually most abundant in spring and early summer, and persisted at low levels during winter. Largest animals (over 2.0 mm long) with high relative caloric content ($\simeq$ 9000 cal g^{-1}) predominated in fall, winter, and early spring when reproduction was minimal. No fish species reside permanently in the pelagic zone of West Blue Lake, but age 0 fry of *Perca flavescens* inhabited the epilimnion during July and early August and fed almost exclusively on *D. pulicaria*. In contrast, age I and older perch consumed a variety of, principally, littoral organisms. Walleye, *Stizostedion vitreum vitreum*, over 25 cm in length put on most of their annual growth in length and weight during the summer, when maximum production also occurred. Perch fry and larger perch were an important food for walleyes.

Ward, F. J., and G. G. C. Robinson. 1974. A review of research on the limnology of West Blue Lake, Manitoba. J. Fish. Res. Board Can. 31: 977–1005.

Les auteurs passent en revue un programme de recherches interdisciplinaires effectuées sur l'écosystème du lac Bleu-Ouest. Ils font rapport sur la composition, la présence saisonnière, l'abondance et la productivité primaire du phytoplancton. Au printemps, la diversité et l'abondance du phytoplancton "tamisé" sont maximales, avec prédominance de diatomées. En été, *Anabaena spiroides* et *Aphanizomenon flos aquae* sont un constituant majeur. En hiver, le nombre de cellules, ainsi que la diversité des espèces diminuent. *Cyclotella bodanica* devient dominant. La productivité primaire estivale du phytoplancton s'est rapprochée de 320 mg C m^{-2} $jour^{-1}$ tant en 1971 qu'en 1972. Les estimés quotidiens

---

[1] This paper, part of a special issue that comprises a comprehensive review of Limnology in Canada, was prepared to mark the 19th Congress of the International Association of Limnology (SIL), in Winnipeg, Man., during August 1974.

Printed in Canada (J3245)

moyens (zooplancton non compris) du carbone organique dans la zone euphotique au cours des mois d'été 1971 et 1972 ont été respectivement de 5 et 8 g C m^{-2}.

Les auteurs donnent les paramètres cinétiques relatifs à la captation bactérienne de 11 substrats organiques dissous. Les valeurs de V_{max} s'échelonnent de 0.003 mg C m^{-3} h^{-1} pour l'acide formique à 0.115 mg C m^{-3} h^{-1} pour l'acide lactique; des temps de renouvellement allant de 8 h pour l'acide malique à 950 h pour l'acide glycolique, et des valeurs de (Km+S) allant de 0.288 mg C m^{-3} pour l'acide malique à 47.883 mg C m^{-3} pour le glucose. Ils décrivent une relation entre les valeurs de V_{max} et les comptages bactériens pour six acides organiques. Ils donnent les signes de prolifération et d'adaptation de la part des bactéries dans les bouteilles d'échantillonnage et de l'absence de photohétérotrophie. La production bactérienne possible, durant l'été 1972, a varié de 18.24 mg C m^{-2} $jour^{-1}$ à 67.44 mg C m^{-2} $jour^{-1}$. On décrit la relation entre cette production et la température (Q_{10} = 3.129). Un "effet filtration," comme source d'erreur, est probablement un phénomène secondaire.

En général, *Cyclops bicuspidatus* est plus abondant que *Diaptomus siciloides*. Les deux sont relativement rares en été. *Daphnia pulicaria* est ordinairement plus abondant au printemps et au début de l'été, et persiste à de bas niveaux durant l'hiver. Les plus grands animaux (de plus de 2.0 mm de longueur) à haut contenu calorique relatif ($\simeq$ 9000 cal g^{-1}) prédominent en automne, en hiver et au début du printemps, alors que la reproduction est minimale. Aucune espèce de poissons ne réside en permanence dans la zone pélagique du lac Bleu-Ouest, mais des alevins de *Perca fluviatilis flavescens* de moins d'un an fréquentent l'épilimnion en juillet et au début d'août, et se nourrissent presque exclusivement de *D. pulicaris*. Par contre, les perchaudes d'un an ou plus consomment une variété d'organismes, surtout du littoral. Les dorés jaunes, *Stizostedion vitreum vitreum*, de plus de 25 cm de longueur subissent la plus grande partie de leur croissance en longueur et en poids au cours de l'été, à l'époque même de production maximale. Les alevins de perchaude et les perchaudes plus grandes sont une source importante de nourriture pour les dorés jaunes.

Accepted December 10, 1973

THIS article describes the scope, nature, and results of research at West Blue Lake since the establishment of the research station in 1965, and indicates relations between components of the ecosystem, evaluating the importance of these relations in defining the productivity of the major components.

West Blue Lake is attractive for an ecosystem study because it approximates a closed system. For example, because the lake has no outlet and only small temporary inlet streams, fish populations are confined; therefore some of the major problems associated with measuring productivity are eliminated. To a much lesser degree this feature simplifies investigations of both phytoplankton and zooplankton.

The station, established under the sponsorship of the University of Manitoba, has dual but interrelated roles: to study and describe the West Blue Lake ecosystem; to provide opportunities for graduate students, specializing in the field of aquatic ecology, to obtain training and experience.

Materials reviewed in this paper are in three categories: previously unpublished data, information contained in accepted student theses, and data abstracted from published papers. Published material receives limited treatment and is used primarily to maintain continuity, to serve as a rationale for other work and, finally, to complete treatment of a particular topic.

Description of the Lake

West Blue Lake is located in Duck Mountain Provincial Park in west central Manitoba (Fig. 1) on the northeastern edge of the Manitoba Escarpment (Davies et al. 1962). The escarpment resulted from shale moraines deposited by the Keewatin ice sheet (Wickenden 1953).

The park is covered by "mixed woods" (Weir 1960). Aspen, white spruce, and balsam fir occupy well-drained sites. A major forest fire in 1961 burned a significant portion of the region. Aspen, balsam poplar, and jack pine are present in the burned region. Black spruce and tamarack stands are located in poorly drained regions.

West Blue Lake (alt 670 m) is apparently the remnant of a meltwater channel which was reoccupied by ice and drift. Final retreat and melting resulted in the formation of a multibasin "channel" lake, a variant kettle type (R. W. Klassen personal communication).

The lake is long, narrow, and steep-sided (Fig. 1). The maximum length is 4.8 km, the maximum depth 31 m, and the mean depth 11.3 m. The area is 160 ha (Bell and Ward 1970). The lake has three main basins (Fig. 1). There is no outlet stream and only two small temporary inlet streams which drain swampy areas to the west of the lake. From 1965 to 1972 lake level has shown a maximum change of approximately 60 cm, although annual fluctuations do not normally exceed 30 cm.

Ice cover usually forms in mid-November, reaches a maximum thickness of about 1 m in early spring, and leaves in mid-May. Depth of snow covering the ice is variable, the maximum recorded being 35 cm.

During the open period, Secchi desk transparency varies between 5 and 10 m. Thermal stratification occurs in late May or early June (Fig. 2). Dissolved oxygen levels remain high above 15 m during most of the open period (Fig. 3), but oxygen is depleted in regions deeper than 20 m during the summer. Circulation may be incomplete. In 1967 oxygen levels were low from 20 m to the bottom even in May, shortly after ice breakup and remained low for the remainder of the summer (Bell and Ward 1970), indicating that spring circulation was incomplete. In late October 1969, oxygen levels approximated 8 mg liter^{-1} from the surface to 26 m. At 30 m there was no detectable dissolved oxygen. This absence of oxygen in the

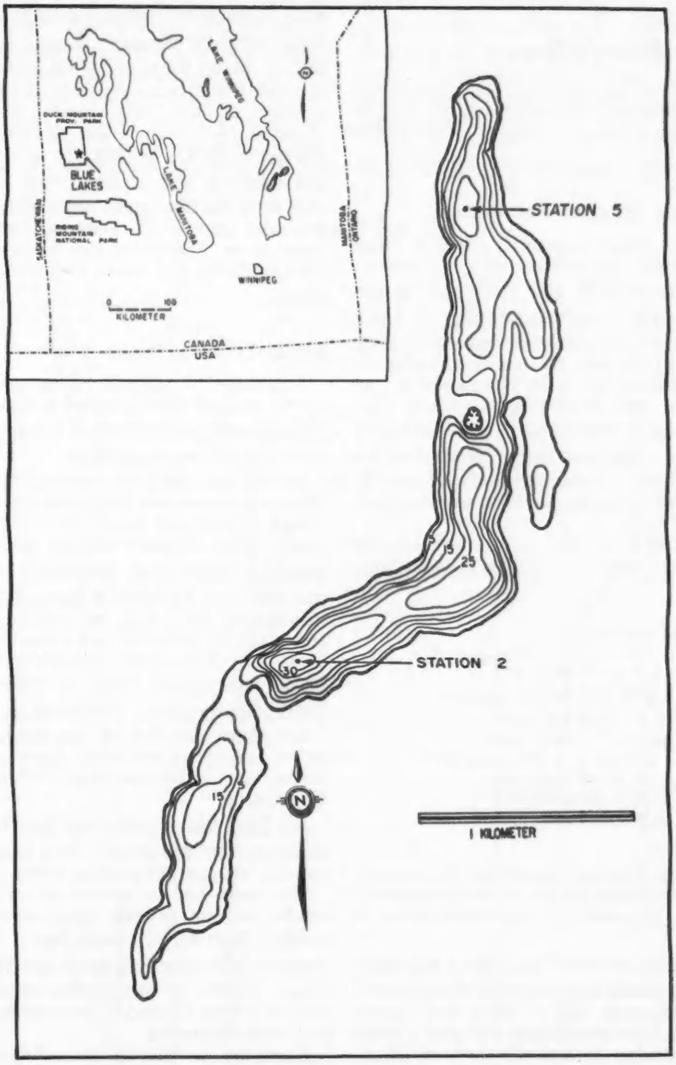

LAKE WINNIPEG
N
DUCK MOUNTAIN PROV. PARK
BLUE LAKES
SASKATCHEWAN
RIDING MOUNTAIN NATIONAL PARK
LAKE MANITOBA
MANITOBA
ONTARIO
WINNIPEG
0
100
KILOMETER
CANADA
USA
STATION 5
15
25
STATION 2
30
15
N
1 KILOMETER

FIG. 1. A contour map of West Blue Lake and its location in Manitoba, Canada, (depths in meters).

deepest water just prior to ice formation is frequent, indicating that fall circulation may also be incomplete in the deepest parts of the lake. Meromixis in West Blue Lake is probably caused by multibasin morphometry and by the direction of prevailing winds.

Total alkalinity expressed as $CaCO_3$ (American Public Health Association 1965) approximates 150 mg liter^{-1} during summer, when the epilimnion ranges from pH 8.0 to 8.6 and the upper hypolimnion has pH values ranging from pH 7.0 to 8.0.

Phytoplankton

Macrophytes are not abundant because of the limited littoral zone (Fig. 1), and were assumed to be less important primary producers than planktonic algae.

COMPOSITION AND RELATIVE ABUNDANCE

Phytoplankters from Station 2 (Fig. 1) were enumerated at weekly intervals during the summer sampling periods in 1970 and 1971 and at approximately monthly intervals during the fall, winter, and early spring. Samples were taken from 0, 3, 7, 12, 17, 20, 25, and 30 m with either a 16-liter Van Dorn sampler or a 30-liter plankton trap (Schindler 1969), and concentrated with a 10-μ Nitex net. Subsamples were counted in a Sedgewick Rafter counting chamber using phase-contrast microscopy. Cell counts were extrapolated to cells m^{-3} and integrated values for the 30-m water column derived.

The following scale is used to represent relative abundance of phytoplankton species in West Blue Lake:

0 – 2.0×10^5 cells m^{-2}
1 – $2.0 \times 10^5 - 1.0 \times 10^6$ cells m^{-2}
2 – $1.0 - 5.0 \times 10^6$ cells m^{-2}
3 – $5.0 \times 10^6 - 1.0 \times 10^7$ cells m^{-2}
4 – $1.0 - 2.0 \times 10^7$ cells m^{-2}
5 – $2.0 - 5.0 \times 10^7$ cells m^{-2}
6 – $5.0 \times 10^7 - 1.0 \times 10^8$ cells m^{-2}
7 – $1.0 - 2.0 \times 10^8$ cells m^{-2}
8 – $2.0 - 3.0 \times 10^8$ cells m^{-2}
9 – $3.0 - 4.0 \times 10^8$ cells m^{-2}

Nannoplankters, passing through the 10 μ screen, may not have contributed much to the phytoplankton biomass, but the extent of any contribution is unknown.

The phytoplankton of West Blue Lake is relatively simple with a predictable seasonal cycle of flagellates, diatoms, and blue-green algae. There are clearly five dominating species throughout the year (Table 1): *Cyclotella bodanica*, *Asterionella formosa*, *Dinobryon sertularia*, *Anabaena spiroides*, and *Aphanizomenon flos aquae*. The spring is characterized by a relatively high number of algal cells and the greatest diversity of the year (23 species in 1970 and 19 in 1971). *Asterionella formosa*, *C. bodanica*, and *D. sertularia* are codominant during this period. These three species alone made up some 45% of the cells in the spring of 1970 and 36% in 1971. This lower percentage in spring 1971 was apparently due to a very early appearance of the blue-green *A. flos aquae*. Although *A. formosa*, *C. bodanica*, and *D. sertularia* persist for almost the entire year, their numbers decrease during the summer and fall, at which times *A. spiroides* and *A. flos aquae* assume dominance. In the summer and fall the number of algal cells remains high although the diversity of species is severely reduced (13 in both 1970 and 1971). During the winter months both cell numbers and diversity drop considerably. At that time the blue-green algae essentially disappear and the diatom *C. bodanica* becomes dominant once more. This is not due to an increase in their own numbers, but rather to a decrease in all other species.

PHYTOPLANKTON PRODUCTIVITY

Estimates of phytoplankton productivity using a ^{14}C method were initiated in the spring of 1967. Subsequently, as sources of error were discovered, our method was modified.

In 1967 and 1968, the radioactivity of ^{14}C labelled algae on membrane filters was determined using a liquid scintillation procedure requiring a toluene-based fluor. Because toluene and water are not miscible, filters were desiccated over soda lime and silica gel for several days. As is now known, desiccation can result in significant and variable losses of ^{14}C (Wallen and Geen 1968; Ward and Nakanishi 1971, 1973). Substitution of a dioxane based fluor (Bray 1960) in 1969 eliminated the desiccation problem. Furthermore, because membrane filters dissolved in this fluor, self-absorption of ^{14}C emissions within the algae on cleared membrane filters in toluene (Pugh 1970)is not a source of error.

We have not adjusted our data for the filtration effect (Arthur and Rigler 1967) because it is probably an artifact (McMahon 1973).

The most serious source of error affecting the results of our primary productivity experiments resulted from use of contaminated ^{14}C solutions in commercially supplied ampoules (Williams et al. 1972). Results of experiments conducted in 1969 and 1970 were affected by particulate contamination and were discarded.

Excretion of ^{14}C-labelled soluble substances by algae during incubation may cause primary productivity to be significantly underestimated (Anderson and Zeutschel 1970). Recently, Schindler et al. (1972) have described a procedure for determining primary productivity which estimates the radioactivity of particulate and soluble organic substances in water samples. We have not determined excretion losses, therefore primary productivity in West Blue Lake has been underestimated by an unknown and probably variable amount.

Experiments were conducted at weekly intervals at Station 2 from ice breakup to the end of August and at approximately monthly intervals during the remainder of the year. Water samples were collected in a PVC water sampler from 0, 1, 3, 5, 7, 12, and 17 m. Paired light and dark 125-ml bottles were filled, inoculated with 1 ml of ^{14}C–NaHCO$_3$ and returned to the lake for 4 h (1000–1400 h). In the laboratory, each sample was filtered through a 0.45-μ Gelman G.A. 6 membrane filter. Scintillation counting procedures, standardization of ampoules, and computation of primary productivity estimates have been described (Ward and Nakanishi 1971). The inorganic carbon content of West Blue Lake water was estimated from alkalinity and dissolved CO$_2$ determinations (American Public Health Association 1965).

Experimental values were extrapolated to daily estimates of primary productivity using the ratio of experimental period incident solar radiation to daily incident solar radiation as measured with a pyrheliometer.

During the late spring and summer of 1972 simultaneous phytoplankton primary productivity

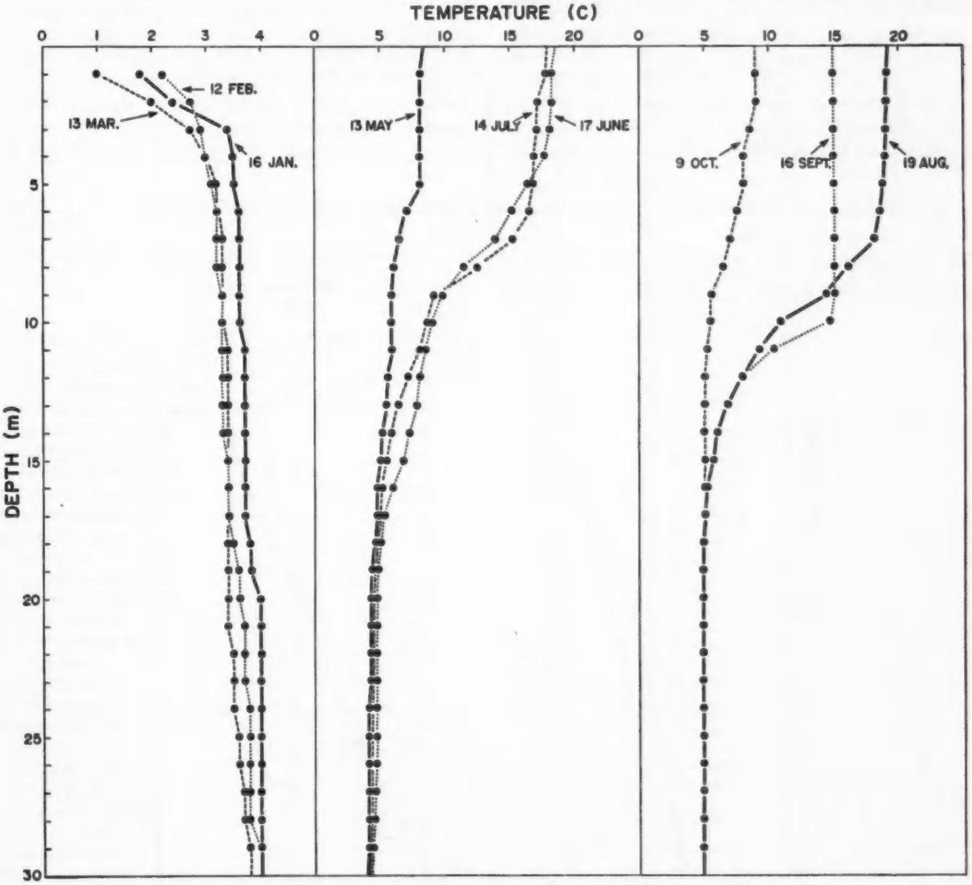


FIG. 2. Temperature profiles in West Blue Lake during 1967.

experiments were conducted at Stations 2 and 5 (Fig. 1) on four occasions. Results (mg C m^{-2} $experiment^{-1}$) were:

	June 8	July 6	Aug. 3	Aug. 24
Stn 2	195	129	82	104
Stn 5	159	123	96	108

Mean productivities at Stations 2 and 5 were, respectively, 127.5 and 121.5 mg C m^{-2} $experiment^{-1}$. The means were not significantly different ($t = 0.214$, NS). Apparently algal primary productivity at widely separated locations was similar.

During 1971 and 1972 primary productivity estimates followed similar seasonal patterns (Fig. 4). When the lake was covered with ice and snow primary productivity was invariably low. For example, January, February, and March values in both years ranged from 0.7 to 36.3 mg C m^{-2} day^{-1}. Productivity beneath thick ice can be significant if the ice is clear of snow so that light penetration is relatively high. For instance on April 17, 1971, productivity was 115.8 mg C m^{-2} day^{-1}.

During both years maximum daily productivity (approx. 800 mg C m^{-2} day^{-1}) occurred in mid-May soon after the ice had left the lake. August productivity was somewhat higher in 1971 than in 1972.

Production during spring and summer (mid-May to late August) in both years was similar, 35.0 and 37.7 g C m^{-2}, respectively. Mean daily productivities were approximately 340 mg C m^{-2} day^{-1} in 1971 and 320 mg C m^{-2} day^{-1} in 1972 during this period. Sampling was insufficient, particularly during fall, for annual production estimates to be derived.

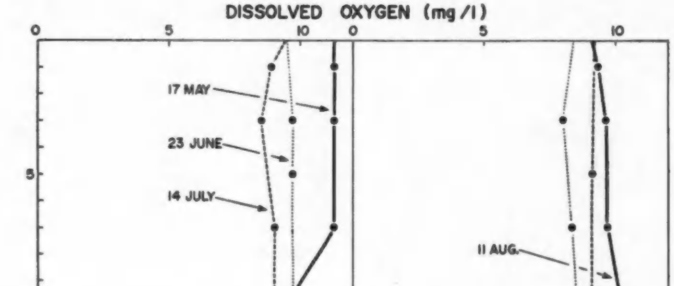


FIG. 3. Oxygen profiles in West Blue Lake during 1967.

STANDING CROP OF PARTICULATE ORGANIC CARBON

The standing crop of particulate organic carbon, exclusive of nekton and zooplankton, was estimated by measurement of the organic carbon content of particles less than 153 μ in diameter present in the water column. In the trophogenic zone, most of these particles were viable algal cells. Water samples of either 1 or 2 liters were collected from 0, 3, 7, 12, and 17 m at Station 2 in 1971 and 1972. Each sample was filtered through a 153-μ Nitex screen to remove larber zooplankters. Some rotifers, protozoans, and eggs passed through into the filtrate. Conversely, masses of *Anabaena spiroides* filaments were sometimes retained on the screen.

Sampling was conducted at weekly intervals from mid-May, soon after ice breakup until the end of August. During the remainder of the year, samples were collected irregularly.

In the laboratory the water samples were filtered through precombusted Whatman GFC filters. The average pore size approximates 1 μ in diameter; therefore most phytoplankters would be retained but some bacterioplankton probably passed through to the filtrate. During 1971 the organic carbon content of material retained on the filters was estimated using a wet combustion method (Strickland and Parsons 1965). In 1972 filters were dried, combusted in a Perkin-Elmer Model 240 Elemental Analyzer, and organic carbon levels recorded. Values determined by the wet combustion procedure were lower than estimates determined using the Elemental Analyzer from replicate samples, indicating, perhaps, that wet combustion of some components of the organisms was incomplete. All 1971 estimates made using the wet combustion method were increased by 30% to make them comparable with the 1972 data measured using the Elemental Analyzer.

Mean organic carbon content of paired samples collected at eight depths (0–30 m inclusive) were 295 and 307 mg C liter^{-1}. These means were not significantly different ($t = 1.129$, df = 4 NS).

Estimates of phytoplankton biomass were compared with particulate carbon values. The correlation between particulate carbon estimates and phytoplankton ash weights was significant ($r = 0.69$, df 13, $P < 0.01$). Particulate carbon estimates were highly correlated with chlorophyll *a* determina-

TABLE 1. Common phytoplankton species and their relative abundance in West Blue Lake as adapted from Cliff 1972.

	Apr.–June 1970	July–Sept. 1970	Oct.–Dec. 1970	Jan.–Mar. 1971	Apr.–June 1971	July–Sept. 1971
Anabaena spiroides	3	8	2	0	4	7
Ankistrodesmus falcatus	1	2	1	0	1	1
Aphanizomenon flos aquae	1	8	3	0	7	9
Asterionella formosa	9	4	4	0	6	4
Botryococcus braunii	1	5	1	0	4	5
Ceratium hirundinella	0	2	0	0	1	2
Crucigenia rectangularis	2	3	1	0	1	0
Cyclotella bodanica	6	6	4	4	7	5
Cymbella sp.	1	0	0	0	0	0
Dinobryon sertularia	6	3	2	1	7	5
Fragilaria capucina	1	0	0	0	0	0
Fragilaria crotonensis	2	0	1	1	2	0
Gloeotrichia sp.	1	0	0	0	0	1
Merismopedia sp.	0	0	0	0	1	0
Navicula sp.	2	1	1	0	3	2
Oocystis elliptica	1	4	0	0	2	1
Oscillatoria sp.	1	0	1	1	0	0
Pediastrum sp.	1	4	0	0	2	1
Peridinium sp.	1	0	0	0	1	0
Phormidium sp.	0	0	1	2	2	0
Pleurosigma sp.	1	0	0	0	0	0
Quadrigula chodatii	1	2	0	0	2	1
Rhizosolenia sp.	1	0	0	0	1	0
Staurastrum sp.	1	0	0	0	0	0
Synedra incurva	2	1	2	0	2	1
Synedra ulna	1	0	0	0	1	0

tion ($r = 0.75$, df 14, $P < 0.01$). Finally, particulate organic carbon content and particulate volume of natural samples and cultured phytoplankton were significantly correlated ($r = 0.78$, df 32, $P < 0.01$).

In 1971, particulate carbon levels beneath the ice were low, generally about 2.0 g C m^{-2} (Fig. 5). The amount of random variability was not estimated although, as shown, replicates were not significantly different. Maximum levels (approx. 10 g C m^{-2}) as with algal productivity occurred in mid-May, soon after breakup. Late spring and summer values averaged about 4.5 g C m^{-2}. The pattern and levels of carbon present above 17 m in 1972 were similar to those of 1971 during early spring but considerably different in summer. Relatively high levels were present in mid-May following breakup, between 8 and 10 g C m^{-2}. Values were then lower (about 7.0 g) until mid-June when they averaged 8.7 g C m^{-2}. The maximum, approximately 10.3 g, occurred during the week beginning July 31. The average daily mid-May-late-August biomass was 5.0 g C m^{-2} in 1971 and 8.1 g C m^{-2} in 1972. Although average spring-summer productivity was similar in 1971 and 1972 (340 and 320 mg C m^{-2} day^{-1}), the standing crop of particulate organic carbon was considerably lower in 1971 than in 1972.

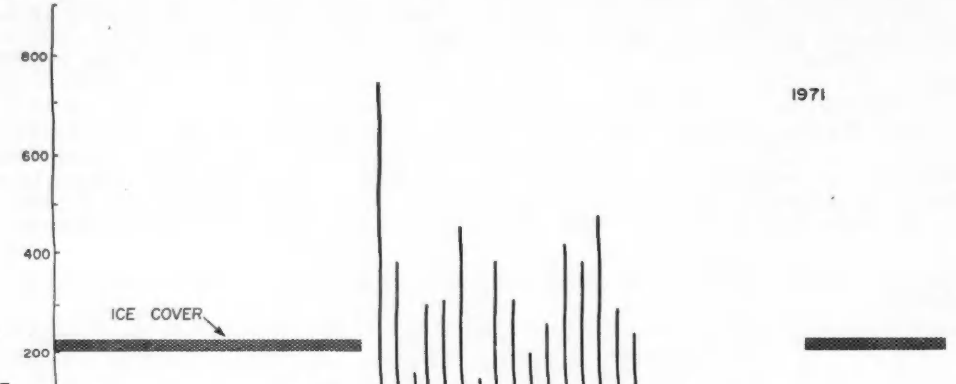


FIG. 4. Rates of phytoplankton primary productivity during 1971 and 1972 at Station 2 in West Blue Lake, Man.

Bacterioplankton

Conceivably bacterial activity in the form of the uptake of dissolved organic matter from lake water provides an intermediate step in pelagic energy routes and leads to mineralization of complex materials. Consequently, an investigation into the utilization of a variety of dissolved organic materials was conducted at West Blue Lake.

UPTAKE OF DISSOLVED ORGANIC COMPOUNDS

During the summers of 1971 and 1972, experiments were conducted on the kinetics of uptake of succinic, pyruvic, lactic, malic, acetic, citric, fumaric, formic, and glycolic acids (Robinson et al. 1973) and of glucose (Robinson et al. unpublished data) and sucrose. The organic acid experiments were conducted at Station 5 (Fig. 1) at 5 m. Experiments with glucose and sucrose were conducted at Station 2 at 3 and 17 m. Our procedure involved the in situ incubation of replicated 25-ml water samples which had been inoculated with increasing amounts of ^{14}C-labelled organic carbon (Robinson et al. 1973b). Velocities of uptake of organic carbon were determined by the method of Parsons and Strickland (1962). For all substrates used there was an apparent active uptake of organic carbon, such that Michaelis–Menten kinetics could be applied. Accordingly, maximum velocities of uptake (V_{max}), turnover times, and (Km + S) values (Km is the Michaelis constant and S the natural substrate level) were derived by the method of Wright and Hobbie (1965, 1966) (Table 2).

The highest maximum velocity of uptake was for lactic acid (0.115 mg C m^{-3} h^{-1}) and the lowest was for formic acid (0.003 mg C m^{-3} h^{-1}). The greatest turnover time was recorded for glycolic acid (950 h) and the shortest for malic acid (8 h). (Km + S) values ranged from 47.88 mg C m^{-3} for glucose to 0.29 mg C m^{-3} for malic acid.

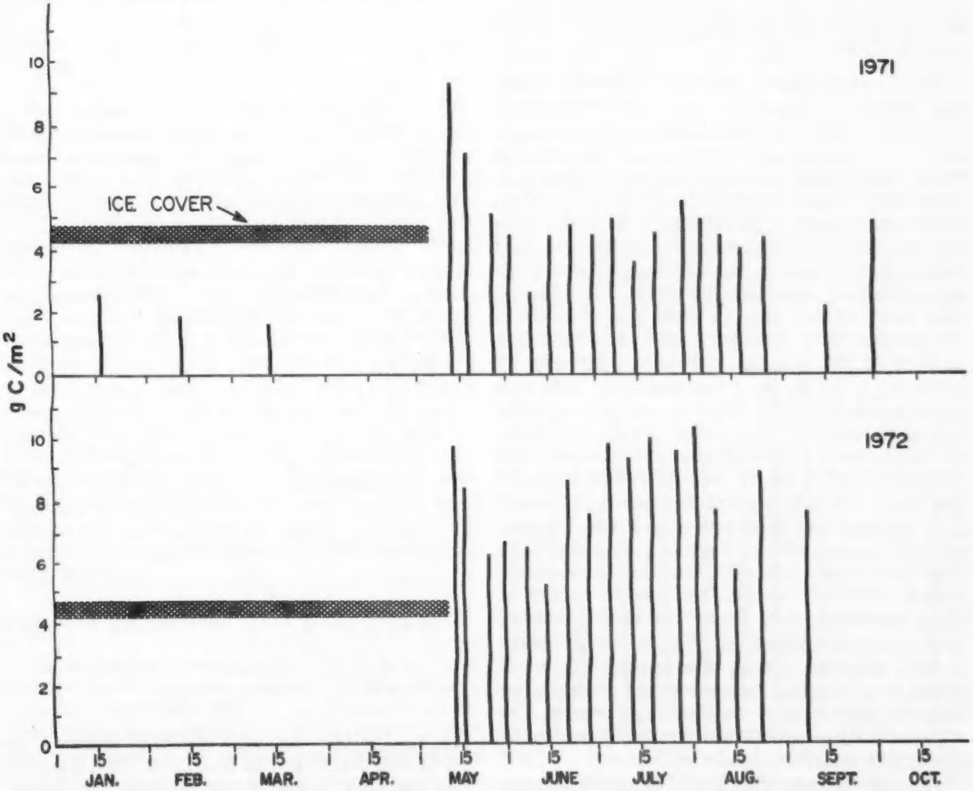


FIG. 5. Particulate organic carbon levels in 1971 and 1972 at Station 2 in West Blue Lake.

TABLE 2. Kinetics of uptake of dissolved organic compounds in West Blue Lake, Man.

Substrate	V_{max} mc C m^{-3} h^{-1}	Turnover time (*h*)	(Km+S) mg C m^{-3}
Acids			
Lactic	.115	303	35.087
Pyruvic	.077	300	23.100
Fumaric	.048	50	2.640
Malic	.036	8	0.288
Acetic	.031	416	13.004
Succinic	.028	33	0.941
Glycolic	.009	950	8.503
Citric	.008	100	0.825
Formic	.003	680	1.768
Glucose[a]	.027	896	47.883
Sucrose	.016	836	13.118

[a]Mean of three experiments.

INFLUENCE OF LIGHT AND INCUBATION PERIOD ON UPTAKE

For the nine organic acids, the influence of light and incubation time upon uptake was investigated (Hendzel 1972). For this purpose an experiment was conducted on each organic acid, in which a water sample was taken from 5 m at Station 5. This sample was passed through a 153-μ Nitex screen to remove zooplankters. Eight 25-ml subsamples were placed in clear glass bottles and eight were placed in similar, but darkened bottles. Four light and four dark cell-free sterile 0.2 μ-filtered lake water control samples were also established. All bottles were inoculated with a nonlimiting amount of ^{14}C organic acid (above the level at which V_{max} for the acid was attained). This substrate amount differed from one acid to another due to differences in V_{max} values for the nine acids. All bottles were then suspended at 5 m in the lake. At intervals of 6, 12, 24, and 48 h, two light and two dark, one light control and one dark control were removed and filtered through 0.45-μ Gelman cellulose acetate filters. Following filtration each filter was rinsed with 100 ml of distilled water to remove adsorbed isotope. The specific activity of filters was estimated by the method used in primary productivity determinations. The net rate of uptake of each substrate at each time interval was determined by subtracting the appropriate control value from the mean dpm of the duplicated sample. The actual velocity of uptake was determined according to Parsons and Strickland (1962).

Although the rates of uptake of the acid substrates differed from each other, for each substrate tested in this way the rate of uptake remained relatively constant for at least 12 h (Fig. 6). For all but glycolic, succinic, and formic acids there was an increase in the velocity of uptake after 12 h, indicating either proliferation or adaptation, or both of the heterotrophic cells within the bottles. Such apparent proliferation or adaptation occurred after 24 h for succinic and glycolic acid and not at all for formic acid. The absence of such a phenomenon on a formic acid substrate was perhaps to be expected because of the chemical nature of this substrate,

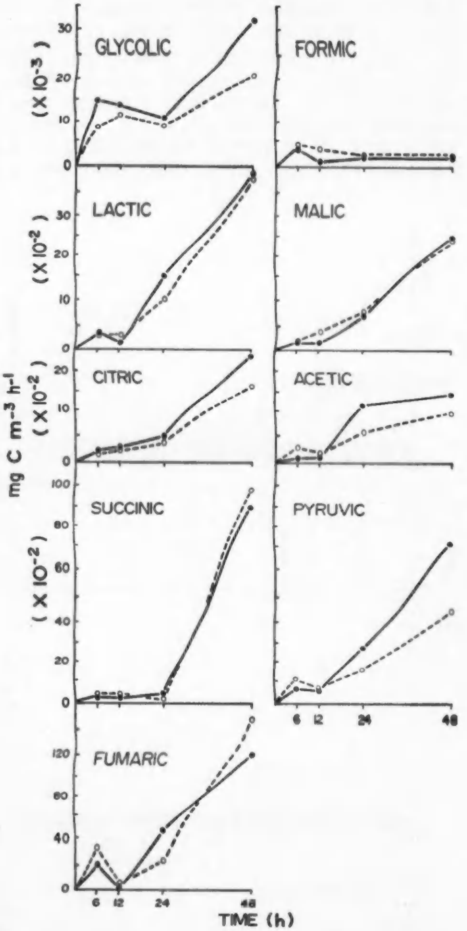


FIG. 6. The light and dark uptake of organic acids over a 48-h period in West Blue Lake, Man. The solid lines represent uptake in the dark and the broken lines, uptake in the light.

which renders it an exceedingly poor energy source. This is also apparent in the excessively low V_{max} value for uptake (Table 2). Such results substantiated the use of a 12-h incubation period for the determination of kinetics of active uptake of the organic acids.

During the first 12 h of incubation there was essentially no difference between light and dark uptake (Fig. 6), indicating the absence of photoheterotrophic mechanisms. During the period of proliferation and adaptation of organisms within the bottles, for glycolic, citric, acetic, succinic, pyruvic, and fumaric acids, there was a difference between light and dark bottles, and in the majority of cases the velocity of dark uptake exceeded the light (Fig. 6). This is perhaps indicative of proliferation of bacteria on the inside of the bottles in the dark as reported by Strickland (1960), during determinations of primary production by use of the O_2 method. Alternatively this might be explained by facultative heterotrophy of photosynthetic organisms in the absence of light.

Relation Between V_{max} and Bacterial Populations

In the absence of a light effect within the first 12 h on velocity of uptake of organic acids, it was hypothesized that the organisms responsible for the uptake were primarily bacteria. To test this hypothesis the numbers of viable bacteria that were capable of growing on single organic acid media were determined by plate counts. These numbers of bacteria supported by single organic acid media, which may represent only a small fraction of the total bacterial numbers, were related to the potential V_{max} values for the uptake of these acids (Robinson et al. 1973). With the exception of lactic and succinic acids and formic acid (which was not tested), there was an excellent correlation between bacterial number and V_{max} values (r = 0.98) (Robinson et al. 1973). Theoretically V_{max} values should be indicative of population size. Therefore, correspondence between bacterial population size and V_{max} for six organic acids certainly indicated that the organisms responsible for uptake were bacteria.

Effect of Temperature on Glucose Uptake

The influence of environmental temperature on the uptake of uniformly labelled ^{14}C glucose was examined (Robinson et al. unpublished data). Throughout the summer of 1972 the uptake of glucose was determined at nonlimiting substrate concentration throughout the 30-m water column at Station 2 (Fig. 1). In onjunction with these determinations, numbers of viable bacteria were assessed by plate counts and water temperature was measured. This permitted the expression of glucose uptake on a per cell basis which could then be related to temperature. There was a direct relation between the two ($r = 0.81$), and a Q_{10} (5.0 – 15.0 C) value of 3.129 for the uptake of glucose was derived (Robinson et al. unpublished data).

Potential Bacterial Production

By integrating values for glucose uptake throughout the water column at Station 2, an estimate of potential bacterial production was made (Fig. 7). During the summer of 1972 this production increased from a minimum value of 18.24 mg C m^{-2} day^{-1} to a maximum of 67.44 mg C m^{-2} day^{-1} by late summer. The individual determinations on which these interactions were based ranged from 0.36×10^{-2} mg C m^{-3} h^{-1} to 23.10×10^{-2} mg C m^{-3} h^{-1} and as such are of the same order as those reported by Wright and Hobbie (1965, 1966) and Allen (1969). Both environmental temperature and plate counts of bacteria contribute to the definition of these production values. The equation for potential bacterial production was:

$$\hat{Y} = 0.0057\,X_1 + 0.0656\,X_2 - 1.9813$$

where $\hat{Y}$ is potential bacterial production (mg C m^{-3} $h^{-1} \times 10^{-2}$); X_1 is plate counts (cells $m^{-3} \times 10^6$) and X_2 is temperature (C). The multiple correlation coefficient was significant ($R^2 = 0.746$, $P < 0.01$). There was no apparent relation between primary production and bacterial production, but

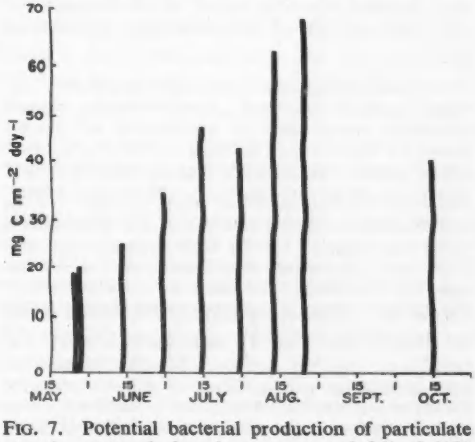


FIG. 7. Potential bacterial production of particulate organic matter during the summer and fall of 1972 at Station 2 in West Blue Lake, Man.

it is noteworthy that the latter may contribute a considerable portion of the particulate organic carbon available to the pelagic food chain. In mid-July the extent of bacterial production was 30.46% of primary production.

Filtration Effect

In all of the above investigations into the uptake of dissolved organic substances, filtration of samples under vacuum was an integral part of procedures. Consequently a "filtration effect" as first described by Arthur and Rigler (1967) may have been operative. Although the existence of such an effect in primary productivity studies is perhaps an artifact (McMahon 1973), the possible application to the use of organic ^{14}C has not been considered.

Two experiments were conducted on West Blue Lake samples to assess the presence and extent of any such effect. Water samples were taken from 3 m at Station 2 (Fig. 1) and a number of 25-ml glass bottles filled. These were inoculated with a standard amount of ^{14}C glucose and suspended at 3 m for a 4-h incubation period. A number of bottles were filled with 0.2 μ-filtered sterile water as cell-free controls. These control bottles were treated in exactly the same way as the experimental bottles. Following incubation, sample bottles were thoroughly mixed together, as were the contents of the cell-free control bottles. Triplicate 1.0-, 2.0-, 3.0-, 4.0-, 5.0-, 7.0-, 10.0-, 15.0-, and 20.0-ml subsamples were removed from the sample mixture and filtered through 0.45-μ membrane filters. For each volume used, a single cell-free control subsample was treated in the same way. All filters were washed with 100 ml of distilled water and the specific activity of each determined as described above.

In both experiments it was apparent that a "filtration effect" did exist. As the volume filtered decreased below 10.0 ml the specific activity retained on the filter per milliliter of filtrate increased. This response was similar to that reported by Arthur and Rigler (1967), Schindler and Holmgren (1971), and Nalewajko and Lean (1972) for experiments using ^{14}C bicarbonate. In both experiments, however, a similar effect was found in the cell-free controls, indicating that such a "filtration effect" may be an artifact as reported by McMahon (1973) for bicarbonate ^{14}C. To determine whether the curvilinear relation between volume filtered and specific activity per milliliter of filtrate were the same for experimental and control samples, a linear transformation of the data was conducted (Fig. 8). Apparently the intercepts of the lines for experimental and control samples were similar, indicating that the "filtration effect" was indeed an artifact, perhaps associated with saturating adsorption of the isotope on the membrane filter.

Zooplankton

Three species of crustacean zooplankters are abundant in West Blue Lake. *Daphnia pulicaria*, originally identified as *Daphnia pulex* (Snow 1972), is the only abundant cladoceran and, in spring and summer, is the dominant component in terms of biomass. *Cyclops bicuspidatus* and *Diaptomus siciloides* are the two common copepods. *Epischura lacustris* and *Mesocyclops edax* are infrequently present in collections. *Bosmina* sp. are rarely present in spring samples. *Chaoborus* sp. are usual in spring and summer samples. *Keratella cochlearis*, *K. quadrata*, *Filinia longiseta* and *Asplanchna* sp. are rotifers often abundant in collections (C. H. Fernando personal communication).

Seasonal Abundance and Size Changes

Beginning in 1967, zooplankton was collected using PVC Van Dorn samplers (4 or 16 liters). In the spring of 1972 and subsequently, sampling

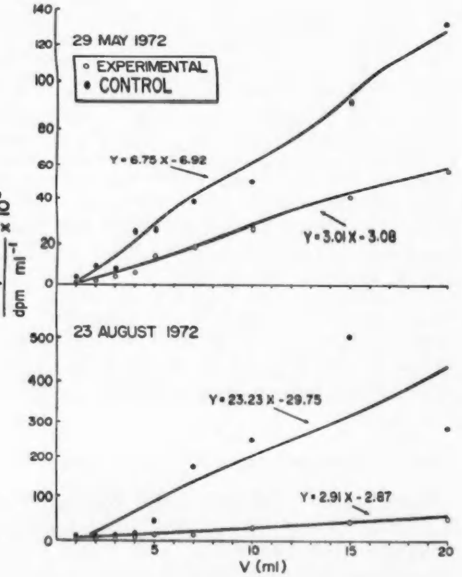


FIG. 8. Linear transformation of the effect of volume filtered (V) upon the apparent uptake of ^{14}C glucose in West Blue Lake, Man.

was done using 30-liter plexiglass plankton traps fitted with 70-μ nylon nets (Schindler 1969). Most samples were collected at Station 2, but in winter and early spring (except for 1970–71) sampling was at Station 5 (Fig. 1). During the first seasons, (1968, 1969, and 1970) the water column was sampled at 5-m intervals from the surface to 30 m, at Station 2, and to 15 m at Station 5. In 1971 the following depths were sampled: 0, 3, 7, 12, 17, 20, 25, and 30 m (to 17 m at Station 5). In 1972 and 1973, 1- and 5-m samples were also collected. Samples were preserved in 5% formalin. All counts were made using a Zeiss inverted microscope and counting cells. Counts were expressed as numbers of individuals at Station 2. Counts from samples collected at Station 5 were multiplied by 1.5, a factor determined by comparing the number of animals in samples collected at the two stations on the same day on nine occasions from May to October 1972.

Zooplankton counts do not necessarily represent true abundance in the lake for a variety of reasons. For instance, horizontal distribution can be affected by wind-produced currents. Secondly, counts made at a single station in a multibasin lake may not be representative of the whole lake. Finally, estimates made at a single deep station may overestimate average abundance in the lake when the animals are concentrated near the bottom.

Lengths of *Daphnia pulicaria* were measured from the center of the compound eye to the base of the caudal spine (Ward et al. 1970). The organic carbon content of *D. pulicaria* was determined from the relation described in Ward et al. (1970).

Copepoda — A complete series of samples was available for the period May 1969–September 1971 (Fig. 9). Adult and late copepodid *Cyclops bicuspidatus* were particularly abundant in the fall of 1969 and winter and spring of 1970. The abundance pattern in 1970–71 was different. *C. bicuspidatus* showed both spring and winter–early spring peaks of abundance. Fall abundance was low (Fig. 9). In all years, including 1968 and 1971, summer abundance was low and, with the exception of 1969, there was a May–June abundance peak of relatively short duration.

The abundance of *Diaptomus siciloides* adults and late copepodids generally followed the trends indicated for *C. bicuspidatus* but they were usually less abundant. May–June peaks occurred in 1968, 1970, and 1971. A fall–winter period of abundance occurred in 1969 and was indicated for 1971 (Fig. 9). As with the cyclopoid, fall abundance in 1970 was low. *Daphnia siciloides* outnumbered *C. bicuspidatus* on several occasions; e.g. mid-August 1968, summer 1970, and late summer 1971.

Daphnia — *Daphnia pulicaria* were always most abundant in spring and summer and relatively rare in late fall and winter (Fig. 9). Reproduction attains a high rate soon after ice leaves the lake and continues during the summer. Population density generally declined in July (with the exception of 1968). Annual differences in spring–summer population abundance were apparent. The 1970 population seemed considerably smaller than populations occurring in other spring–summer seasons.

Large, red, fat-laden overwintering *D. pulicaria* frequently contained eggs in late winter and embryos in early spring before ice breakup. Probably these overwintering females produce the first generation of the new season. In contrast to animals in summer, these winter animals contained many young and as many as 15 eggs per female were frequent. Animals with developing ephippia are present in samples collected in late summer and autumn but they always seem to form a relatively small proportion of the population. Animals bearing ephippia have also been observed during the spring. Dr N. B. Snow (Univ. Manitoba, Winnipeg, Man., personal communication) noted a heavy mortality in *D. pulicaria* beneath the ice on April 17, 1971. He observed large numbers of dead on the surface and animals in the 0-m collection were dead.

In early spring immediately following ice breakup large *D. pulicaria* frequently have an epiflora and epifauna. In mid-May 1973 many *Synedra* sp. were attached to the exoskeletons of the largest *D. pulicaria*, giving them a "furry" appearance. In previous springs we have observed numerous *Vorticella* sp. attached to both *D. pulicaria* and to the copepods.

The modal size of *D. pulicaria* changed from 2.4 mm in February 1970 to 1.4 in May (Snow 1972). The size change was associated with the production of young. Snow noted that the size distribution was bimodal in June and predominantly unimodal during the remainder of the summer (2.0–2.4 mm). In January, February, and March 1971, only the largest individuals remained. Size changes reported by Snow for 1970–71 were similar in 1972–73 (Fig. 9). The average length of animals was minimal (about 1 mm) in mid-May in both 1972 and 1973. Mean lengths increased in June 1972 to approx. 1.8 mm and remained at this level during the summer. Mean lengths increased during the fall of 1972, reaching a maximum of 2.6 mm in January and February 1973.

The caloric content of *D. pulicaria* in West Blue Lake was affected by animal size and season (Snow 1972). Large winter animals had a high energy content (ca. 9000 cal. g^{-1} dry wt) whereas smaller animals sampled at the same time had caloric contents of about 5000 cal g^{-1} dry wt. Animals of all sizes sampled during late spring, summer, and early fall had caloric contents similar to those of the small winter animals (ca. 5000 cal g^{-1} dry wt). Snow (1972) suggested that the high caloric content of the large winter animals placed them in "an advantageous position with respect to the early production of young as soon as conditions become

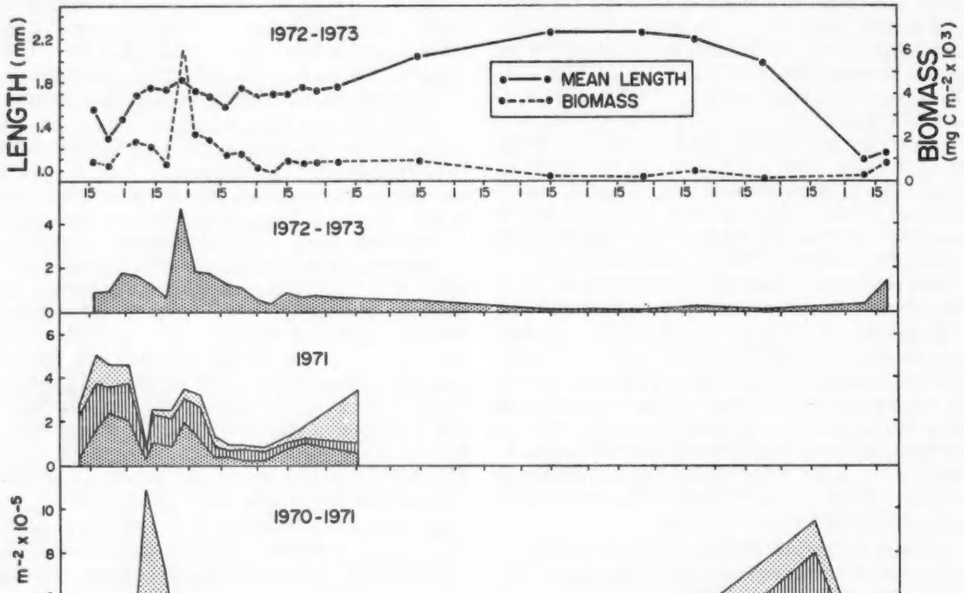


FIG. 9. Seasonal abundance of three zooplankters and seasonal biomass estimates and mean sizes of *Daphnia pulicaria* in West Blue Lake.

favorable." This high energy content may relate to the observed large number of eggs and embryos seen in these large *D. pulicaria* as noted above.

Daphnia pulicaria counts converted to biomass (g C m^{-2}) using the 1972–73 counts and mean lengths indicated a mid-May to late August biomass of 1381 g C m^{-2}. Individual biomass estimates (Fig. 9) were highly correlated with counts as expected. The presence of primarily large individuals in winter did not compensate for their relative scarcity.

FEEDING OF *Daphnia pulicaria*

Because *D. pulicaria* is the major herbivore of the spring–summer zooplankton and an important source of energy for small fish (Wong 1972; Falk 1971), efforts have been made to estimate their productivity and feeding ecology.

Effect of diel migration on incorporation rates — In 1967 and 1968 a series of in situ and tank experiments was conducted to estimate incorporation of organic carbon by *D. pulicaria* from different concentrations of ^{14}C-labelled natural phytoplankton and at 15, 20, and 25 m using ^{14}C-labelled artificial detritus. This artificial detritus may have had a lower nutritive value than the natural substance because it was sterilized. Because of the depth variations and because experiments were carried out in May, June, July, August, and early September, experimental temperature was a variable as well as food type and concentration. The in situ experiments were designed with consideration for endogenous diel rhythms (Bell and Ward 1970). The experiments conducted in tanks located on shore were designed primarily to examine the effect of a wide range of food concentrations on incorporation rates (Bell and Ward 1970).

From these experiments two equations were developed to define incorporation by *D. pulicaria* (mean carbon content 16.4 μg C $indiv^{-1}$). The equation for incorporation of organic carbon from ^{14}C-labelled natural phytoplankton was:

$$\hat{Y} = 0.0002\,X_1 + 0.0314\,X_2 - 0.1893$$

where X_1 was food concentration (μg C $liter^{-1}$) X_2 was temperature (C), and $\hat{Y}$ was the incorporation rate (μg C $indiv^{-1}$ h^{-1}). The multiple correlation coefficient was significant ($R = 0.667$, $P < 0.01$). The comparable equation for incorporation from artificial detritus was:

$$\hat{Y} = 0.0739 \log X_1 + 0.0072\,X_2 - 0.1401.$$

The multiple correlation coefficient was highly significant ($R = 0.881$, $P < 0.01$).

We used these two equations to estimate the effects of varying diel migration patterns on incorporation rates and on the role of detritus in nutrition (presuming our sterilized artificial detritus was similar to the natural counterpart). In general, detritus contributed less than 17% of the estimated daily total of incorporated organic carbon. In contrast, phytoplankton contributed between 84 and 88% of daily totals. However, total daily incorporation rates varied from 2.37 to 5.35 μg C $indiv^{-1}$ depending on the diel migration model used. During thermal stratification, diel migration patterns defined the daily temperature regimes affecting the animals and, therefore, incorporation rates.

These experiments were deficient in several ways. Firstly, because we initially determined the radioactivity of whole dried *Daphnia*, self-absorption of ^{14}C within the experimental animals had to be estimated. A self-absorption coefficient was determined using an in-vial dry combustion technique (Bell and Ward 1968). Subsequently, it was found that self-absorption coefficients were a function of animal size (Ward et al. 1970). The present use of a digestant such as NCS has obviated the need for a time-consuming combustion procedure (Ward et al. 1970).

Secondly, incorporation rates determined with labelled natural phytoplankton were more variable than those determined with animals fed artificial detritus (Bell and Ward 1970). These differences may have been caused by seasonal changes in the composition of the natural phytoplankton. Selection or rejection of an important component could have affected the relation between incorporation rate and total food concentration (Bell and Ward 1970).

Finally, analyses of data from the experiments concerning variations in self-absorption coefficients with size also indicated that incorporation rates varied with animal size. Consequently, seasonal changes in the mean size of individuals and in the size-frequency distribution of the population could affect incorporation rates and *D. pulicaria* productivity.

Effect of animal size and food type on incorporation rates — During 1970 and 1971, a series of laboratory experiments using ^{14}C-labelled food was carried out to determine the relation between food type, animal size, and incorporation rates.

In five experiments conducted at 12 C, *D. pulicaria*, grouped by length, were placed in nonaxenic, labelled algal cultures. The foods were *Chlorella vulgaris*, *Ankistrodesmus falcatus*, *Navicula pelliculosa*, *Anabaena spiroides*, and a natural mixture of phytoplankton sampled from the lake. The dominant species in the natural sample were *A. spiroides* and *Dinobryon sertularia*. Basic experimental procedures, outlined below, were similar to those described by Sorokin (1966) and modified by Bell and Ward (1970), Ward et al. (1970), and Narita and Ward (1972): 1, determination of the specific radioactivity and organic carbon content of labelled food cultures (including controls); 2, addition of animals; 3, incubation; 4, transfer of animals to unlabelled cultures for 2 h to clear the alimentary tract of labelled food; 5, determination of the specific radioactivity and particulate carbon content of both experimental and control cultures after feed-

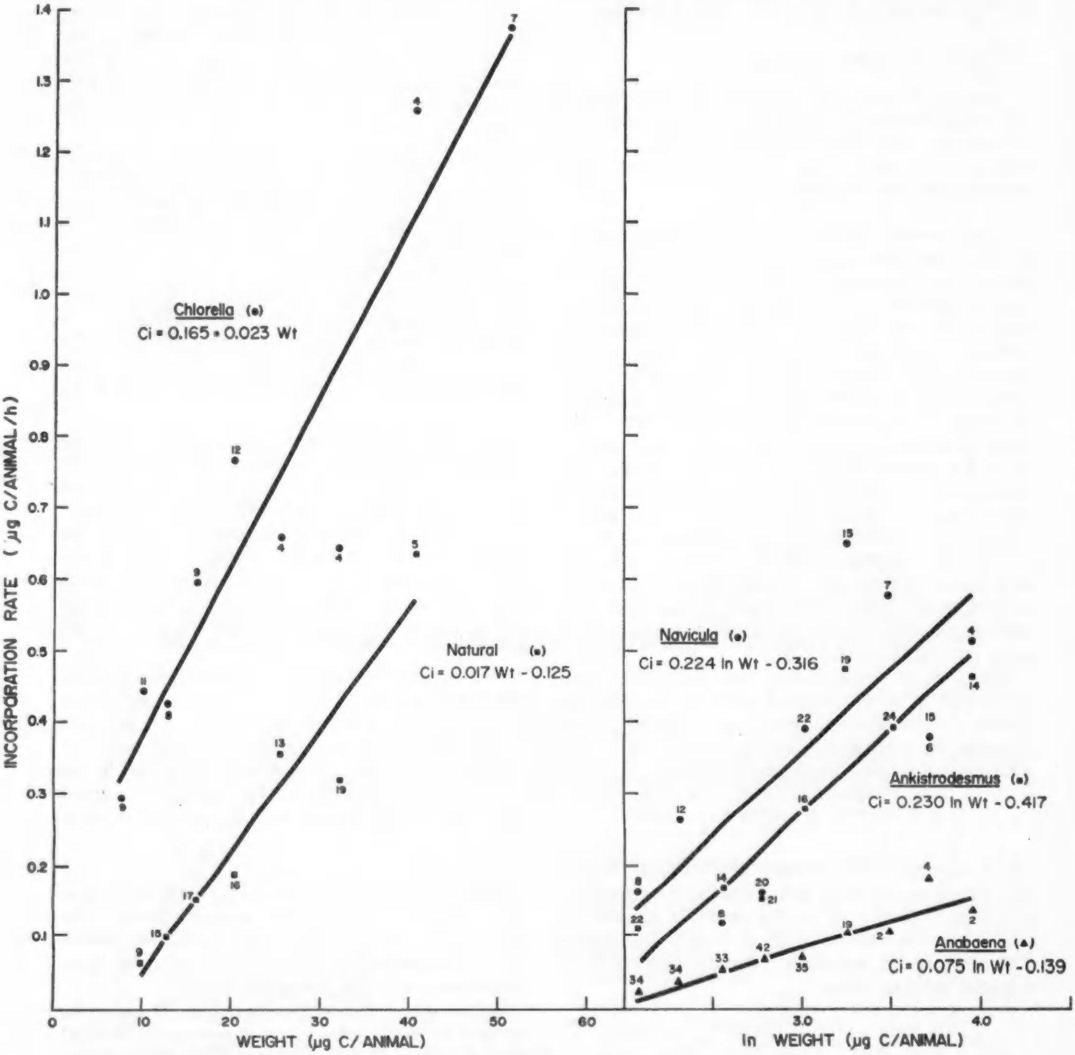


Fig. 10. Relationship between *D. pulicaria* size and incorporation rates for various foods. Numbers near points represent the number of experimental animals.

ing; 6, removal of animals from the clearing culture, digestion in a strong base, addition of fluor, and determination of specific radioactivity.

All five regression coefficients calculated from the relations between the body carbon content of *D. pulicaria* and incorporation rates (Fig. 10) differed significantly from zero. For the *Anabaena*, *Ankistrodesmus*, and *Navicula* data, transformation to the natural logarithms of body carbon content resulted in reductions in the deviations from regression (Fig. 10). Coefficients of determination (r^2) ranged from 0.55 to 0.88, indicating that even in animals fed *Navicula* sp. the regression accounted for more than half of the variability in incorporation rates.

Incorporation rates were highest for animals fed *Chlorella*, and intermediate for those fed *Navicula*, the natural mixture, and *Ankistrodesmus*. Incorporation rates were uniformly low in animals fed *Anabaena* (Table 3).

The mean size of *D. pulicaria* (μg C indiv^{-1}) in samples collected from West Blue Lake tended to increase during the summer of 1970 (Table 4). These mean sizes were used to calculate incorporation rates using the equations determined for each food type (Fig. 10). For all food types, the maximum seasonal size change caused major differences in estimated incorporation rates (Table 4). The greatest effect was produced by the use of the natural mixture.

These results indicate that incorporation of organic carbon invariably increased with animal size, but relations vary depending on food. In our experiments *Chlorella* was apparently a good food, but *Anabaena* (as also reported by others) was a poor one. In fact, we calculated that incorporation of *Anabaena* provided insufficient energy even for respiration, whereas the other foods all provided large excesses of energy incorporated over energy respired. Our results also indicate that seasonal size changes in the *D. pulicaria* population might significantly affect population incorporation rates.

Effect of animal size on ingestion rates — During the summer of 1970 we attempted to measure ingestion rates of different sizes of *D. pulicaria* placed

TABLE 3. Incorporation rates for *Daphnia pulicaria* of various sizes showing 0.95 P confidence intervals.

Body carbon (μg)	Incorporation rates (μg C animal^{-1} h^{-1})				
	Anabaena	*Ankistrodesmus*	Natural	*Navicula*	*Chlorella*
7.9	.016±.027	.058±.102		.147±.203	0.347±.166
10.0	.033±.022	.113±.085	.045±.094	.200±.169	0.395±.154
12.7	.051±.018	.168±.070	.091±.082	.253±.139	0.458±.140
16.0	.069±.016	.221±.059	.147±.070	.305±.118	0.533±.125
20.2	.086±.015	.274±.055	.218±.061	.357±.110	0.630±.113
25.5	.104±.016	.328±.059	.308±.062	.409±.118	0.752±.109
32.2	.121±.018	.381±.070	.422±.082	.462±.139	0.908±.126
40.7	.139±.022	.435±.085	.567±.121	.514±.169	1.102±.169
51.4	.156±.027	.489±.102	–	.566±.203	1.348±.239

TABLE 4. Estimated incorporation rates (μg C animal^{-1} h^{-1}) calculated from food regression equations for mean sizes of *Daphnia pulicaria* (0.95 confidence intervals shown) from West Blue Lake during 1970.

Date	Mean wt (μg C animal^{-1})	Food				
		Anabaena	*Ankistrodesmus*	Natural	*Navicula*	*Chlorella*
June 17	8.83±0.79	.024	.084	.025	.172	.368
July 1	12.84±1.29	.052	.170	.093	.256	.460
July 15	9.23±0.75	.028	.094	.032	.182	.377
July 29	12.10±1.03	.048	.156	.081	.242	.443
Aug. 12	13.00±1.50	.053	.173	.096	.259	.464
Aug. 25	15.49±0.91	.067	.213	.138	.298	.521
Maximum increase (%)		179	157	452	73	42

in *Ankistrodesmus falcatus* cultures (approximately 500 μg C liter^{-1}). Steps in the experiment were: 1, measurement of particle numbers and the size distribution of particles in each culture prior to the introduction of the animals; 2, introduction of one size-group of animals to each culture flask (500 ml); 3, removal of the animals at the end of 4 h and determination of the number and size distribution of remaining particles; 4, calculation of the number of particles ingested per animal from the difference in particle number in cultures before the introduction of animals and after their removal. This former number was adjusted for growth of the food, as determined from changes occurring in cultures in control flasks without animals. The numbers and size distribution of particulate matter in the *A. falcatus* cultures were determined using a Model B Coulter Counter with "J" Plotter.

The relation between *D. pulicaria* size (X) and particle ingestion rate ($\hat{Y}$), $\hat{Y} = 92.48 + 15.32\,X$, was highly significant ($r = 0.94$, df = 7, $P < 0.01$), but there was little evidence for particle size selection by animals of different sizes (Table 5). The mean volume of individual particles consumed was relatively similar for the largest and the smallest animals even though their sizes, in terms of body carbon content, varied by a factor of over 6.

This single experiment does not indicate that selection for a particular range of particle sizes is unrelated to animal size nor that selection is unimportant in nature. The size range of particles available in these monocultures was limited (from 200 to 1400 μ^3). Furthermore, palatability may play a role in size selective feeding.

TABLE 5. Number and mean volume of particles consumed by *Daphnia pulicaria* of various sizes from 1 ml of a series of *Ankistrodesmus falcatus* cultures.

Animal size (μg C indiv.$^{-1}$)	Particles consumed	
	No. indiv.$^{-1}$ ml^{-1}	Mean vol (μ^3) *of individual* particles
8(20[a])	237	417
10(8)	351	387
13(16)	276	328
16(23)	310	357
20(17)	384	416
26(19)	480	422
32(24)	496	400
40(15)	586	392
51(17)	1022	453

[a] The number of animals in each experimental size-group.

Fish

Five species of fish are present in West Blue Lake but only two are abundant, the yellow perch (*Perca flavescens*) and the walleye (*Stizostedion vitreum vitreum*). Northern pike (*Esox lucius*) and brook stickleback (*Culaea inconstans*) are much less numerous. Lake trout (*Salvelinus namaycush*) were introduced prior to 1967 but only a few now survive.

Walleye are an important commercial species in Manitoba. For this reason they have been most intensively studied. Initial research concentrated on defining relative abundance, food, age distribution, and seasonal growth (Glenn 1969). More recently, effort has been concentrated on population enumeration and seasonal productivity (Kelso and Ward 1972).

Perch are an important food for walleye during summer (Glenn and Ward 1968). Consequently, the feeding habits and general biology of perch have been studied. Wong (1972) and Wong and Ward (1972) reported on the early life history, growth, and feeding of age 0 perch fry. Falk (1971) described food habits and consumption of older perch.

FOOD AND FEEDING OF AGE 0 PERCH FRY

Capture, preservation, length measurement, mouth dimensions, and stomach content analyses procedures for perch fry have been described (Wong and Ward 1972). Diel changes in the vertical distribution of fry were determined from catches made using a surface tow net modified to fish at depths of approx. 3 and 5 m by the addition of weights and a paravane. The net was calibrated by its ability to catch objects suspended at known depths. Wet weights were determined to the nearest 0.05 mg. Perch fry less than 20 mm total length were weighed in groups but larger fish were individually weighed.

The organic carbon content of perch fry and food organisms other than *D. pulicaria* was determined using a wet combustion method (Strickland and Parsons 1965). Organic carbon values for *D. pulicaria* of various lengths were available (Ward et al. 1970). Prior to treatment, copepods were divided into two groups: 1, adults plus copepodids and 2, nauplii. Amphipods were divided in six size classes (0.5-mm intervals). Amphipod length was measured, using a microscope fitted with a measuring eyepiece, from the center of the eye to the tip of the telson, with the body straightened.

Calorific values for perch and their food organisms were obtained using a modified Phillipson calorimeter (Snow 1972).

Soon after hatching in late spring and early summer, West Blue Lake perch fry (about 8.0 mm total length) move offshore from the spawning areas and occupy the epilimnion. Initially they are dark on the dorsal surface but the sides are almost transparent. As they grow the sides become silvery. Throughout the early summer in both 1969 and 1970, fry were readily captured in the evening near the surface in mid-lake using the surface tow net. In early August when the fry were about 30 mm long and were developing the typical "barred" color pattern of the adults, mid-lake catches declined abruptly but increasing numbers of fry were observed and captured by seining in the littoral zone. Catches per 5-min tow in 1969 are given below:

July 1	42	Aug. 3	42
July 2	38	Aug. 6	23
July 4–27	>50	Aug. 8	10
July 30	49	Aug. 10	5
Aug. 1	34	Aug. 15	0

The disappearance of fry from the epilimnion was supported by evidence from echograms (Wong 1972). A band of echoes associated with tow-net catches of perch disappeared from echograms of the epilimnion at the time that tow-net catches decreased in early August and fry became abundant in the shallows.

Largest catches of perch fry using the surface tow net were made after sunset in 1969 (Wong 1972). These data indicated that perch fry were more vulnerable in the dark and there was a diel vertical migration.

Catches using tow nets set at three depths indicated that there was a rather limited diel migration (Table 6) between 0 and 5 m. Percentages of total catches were generally low during daylight at the surface (5.5–36.2% of totals). Exceptions were the 0500 and 0700 catches of June 30. In contrast, catches made at the surface after sunset on June 29 constituted the major fraction of total catches. Conversely, daylight catches at 5 m on June 29 were relatively higher than at the surface. Again, exceptions were the 0500 and 0700 catches of June 30.

Length and weight data from 1251 age 0 perch fry collected in 1969 demonstrated that perch fry more than tripled their length and increased their weight by a factor of 9 from July 1 to August 31. The average increments were 3.8 cm and 1.8 g. The regression equation for growth in total length was: $\ln L_t = \ln L_o + 0.022t$ where L_o and L_t were, respectively, initial and final lengths (cm) and t was time in days. The comparable weight equation was: $\ln W_t = \ln W_o + 0.074t$. Both regression equations were statistically significant. For the length equation, $H_o : b = 0$ could be rejected ($F = 75$, df = 1 and 29, $P < 0.01$) and similarly for the weight equation $F = 773$, df = 1 and 29, $P < 0.01$.

The length–weight relation for the same group of fish was: $\log W = 3.4 \log L - 2.6$, where length and weight were measured in mm and mg. This equation was also highly significant ($F = 3703$; df = 1, 29, $P < 0.01$).

Items in stomach contents of perch fry were expressed in caloric values and in terms of their organic carbon content. The caloric and carbon

TABLE 6. Yellow perch (*Perca flavescens*) fry caught by 5-min tows at 0-, 3-, and 5-m depths on June 29 and 30, 1970.

	Depth (*m*)						
	0		3		5		
Time	No.	%	No.	%	No.	%	Total
0900	4	10.8	14	37.8	19	51.4	37
1100	4	5.5	36	49.3	33	45.2	73
1300	5	12.5	19	47.5	16	40.0	40
1500	5	10.6	22	46.8	20	42.6	47
1700	5	20.8	12	50.0	7	29.2	24
1900	42	36.2	35	30.2	39	33.6	116
2100	83	62.9	22	16.7	27	20.5	132
2300	532	62.7	188	22.1	129	15.2	849
0100	220	43.3	168	33.1	120	23.6	508
0300	134	49.1	78	28.6	61	22.3	273
0500	97	67.8	27	18.9	19	13.3	143
0700	48	67.6	15	21.1	8	11.3	71

contents of *D. pulicaria* were, respectively, 4917 calories g^{-1} dry weight and 461 mg C g^{-1} dry weight. The body-length carbon content relation (Ward et al. 1970) was used to determine the caloric values of *D. pulicaria* of different sizes. The caloric and organic carbon contents of adult copepods were, respectively, 0.0224 cal and 1.56 μg C. For nauplii the comparable estimates were 0.0038 cal and 0.32 μg C. The relation between amphipod length and body carbon content was: $\log Y = 1.248 + 0.207 X$, where X is amphipod length (mm) and Y is organic carbon content (μg). This relation was statistically significant ($r = 0.96$, df $= 4$, $P < 0.01$). Similarly the relation between body length (X) and caloric content Y ($Y = 0.697 X - 0.398$) was significant ($r = 0.99$, df $= 4$, $P < 0.01$). Caloric values and organic carbon values for perch fry flesh were, respectively, 4967 cal g^{-1} dry weight and 422 mg C g^{-1} dry weight.

During the summer of 1969 age 0 perch fry utilized a narrow range of food items, primarily zooplankton. *Daphnia pulicaria* occurred in all but a few of stomachs examined (Table 7). Copepods, *Cyclops bicuspidatus* and *Diaptomus siciloides*, occurred less frequently. Amphipods, *Gammarus lacustris* and *Hyalella azteca*, occurred only in perch fry sampled in August after the fry had moved inshore from the epilimnion. Traces of plant material were found in small fry captured early in the season. This material may have been inadvertantly ingested along with zooplankters or was present in guts of ingested zooplankters. Dipteran pupae rarely occurred in perch fry stomachs during early July (frequency of occurrence was less than 0.5%). Other rare items were an ostracod and one unidentified fish larva.

Considering contributions to the total energy contained in stomach contents, *D. pulicaria* was always dominant. Average contributions ranged from 77% in early summer to 96% in mid-August (Table 7). Copepods were a significant energy source, their contributions ranging from 19% early in the season to less than 1% in late August. Nauplii and amphipods contributed minor amounts of energy.

Not all sizes of *D. pulicaria* were fully utilized by perch fry. Prior to mid-July, *D. pulicaria* in fry stomachs were smaller than those found in plankton collections (Wong and Ward 1972), indicating an initial size selection for small *D. pulicaria*. Subsequently mean sizes of the cladoceran in stomachs and in the plankton catches were similar. Apparently *D. pulicaria* longer than 1.3 mm could not be readily ingested by perch fry until mid-July, when the fry were approximately 18 mm long.

Ratios of mouth gape width to body length in the perch fry indicated that growth in mouth size was more rapid than growth in body length. This heterogonic relation between mouth and body growth permitted early utilization of relatively large food items.

FOOD OF JUVENILE AND ADULT PERCH

Perch 1-yr-old and older were caught in nylon thread gillnets with mesh sizes (stretched measure) of 19.1, 25.4, 38.1, and 50.8 mm set at depths ranging from 1 to 10 m. Netting sites were located in relatively shallow areas in all three basins (Fig. 1). Generally, nets were set before sunrise and hauled every 2 h throughout the day until no perch were caught. Fish were weighed to the nearest 0.1 g. Total and fork length were recorded. Catches were separated into two major groups, juveniles (<120 mm fork length) and adults (>120 mm fork length).

TABLE 7. Percent frequency of occurrence of items in perch fry stomachs (columns 1) and their percentage contribution to mean total caloric content of each stomach (columns 2).

Date	*Daphnia*		Copepods		Nauplii		Amphipods	
	1	2	1	2	1	2	1	2
July 1–5, 1969	99.9	86.9	58.6	13.2	–	–	–	–
July 6–12	100.0	87.5	26.8	12.5	–	–	–	–
July 13–19	100.0	91.3	13.6	8.7	–	–	–	–
July 20–26	100.0	94.5	23.3	5.5	–	–	–	–
July 27–Aug. 2	100.0	93.9	25.5	6.1	–	–	–	–
Aug. 3–9	100.0	94.0	38.7	6.0	–	–	–	–
Aug. 10–16	100.0	96.1	42.1	3.9	–	–	–	–
Aug. 17–23	100.0	92.5	25.0	2.6	–	–	65.6	4.5
Aug. 24–30	100.0	94.3	21.2	0.6	–	–	40.4	5.1
June 15–29, 1970	100.0	77.1	100.0	19.2	100.0	3.7	–	–

Food organisms were identified, counted, and weighed (wet weight) to the nearest mg.

In contrast with age 0 perch during their pelagic phase, older perch were active only during the day. Greatest catches were usually made in early evening (Falk 1971). Perch were never caught at night. Using a spotlight, perch were observed lying on the bottom, often among submerged vegetation. Falk (1971) also noted that perch tended to inhabit deeper water in the morning and shallower water in the evening. Similarly small perch tended to be in shallower water than the adults. Catches at the same location varied seasonally indicating that relative abundance changed.

With some exceptions, indices of stomach fullness for both juvenile and adult perch were bimodal, with morning and evening peaks and afternoon lows in stomach contents (Falk 1971). Keast and Welsh (1968) also found that perch had two daily periods of maximum stomach fullness.

During the summer of 1970 the major food of juvenile yellow perch were the two amphipod species, *Hyalella azteca* and *Gammarus lacustris* (Table 8). *Daphnia pulicaria* was a major component in late June and mid-September. The brook stickleback (*Culaea inconstans*) was a major component in August. In contrast, among adult perch in 1969 (Table 9), amphipods were the major food

TABLE 8. Percentage by weight of major food items in juvenile perch stomachs during 1970.[a] The wet weight of stomach contents is given beneath each date. Numerals in parentheses are the number of items.

Item	*June 23–24* 2.74 g	*July 21–22* 7.83 g	*Aug. 24–26* 3.98 g	*Sept. 14–16* 5.37 g
Hyalella	11(76)	46(1280)	21(566)	4(86)
Gammarus	23(22)	23(285)	9(46)	8(36)
Daphnia	32(3363)	0	0	69(15,053)
Diptera	*11(123)*	*1(17)*	*1(6)*	*1(31)*
Hemiptera	0	0	0	0
Perca	3(7)	29(24)	30(1)	0
Orconectes	0	1(2)	7(3)	10(1)
Culaea	10(1)	0	30(6)	1(2)
Other insects	10(17)	1(8)	3(5)	0
Others	0	0	0	8(9)

[a] The number of perch containing food in June, July, Aug., and Sept. samples were 72, 124, 49, and 86.

TABLE 9. Percentage by weight of major food items in adult perch stomachs during 1969.[a] The total wet weight of stomach contents is given beneath each date. Numerals in parentheses are the number of items.

Item	June 8–9 8.24 g	June 22 30.38 g	July 23–24 20.44 g	Aug. 24–25 11.40 g
Hyalella	60(929)	1(19)	1(9)	1(56)
Gammarus	11(31)	5(51)	11(115)	8(246)
Daphnia	0	5(4541)	0	2(459)
Diptera	25(831)	52(3261)	1(3)	0
Hemiptera	0	1(4)	1(16)	0
Odonata	0	18(18)	5(10)	0
Perca	0	0	8(5)	14(3)
Orconectes	2(1)	0	5(9)	54(5)
Culaea	0	20(6)	41(16)	19(13)
Other insects	3(7)	0	0	3(1)
Others	1(1)	0	30(4)	0

[a] The number of perch containing food in June 8–9, June 22, July, and Aug. samples were 31, 87, 71, and 51.

in the early June sample only. Diptera were major items in June but were replaced by the stickleback, crayfish, *Orconectes virilis*, and diptera (principally *Chaoborus* sp.) pupae. *Daphnia pulicaria* were never a major food for adult perch.

Juvenile perch caught at depths between 0 and 5 m in 1969 fed mainly on *Hyalella* and to a lesser extent on *Gammarus* and sticklebacks. Perch caught between 5 and 10 m had fed on *Gammarus* and to a lesser extent on *Hyalella* and immature dipterans (Falk 1971).

Biette (1969) found abundance of both *H. azteca* and *G. lacustris* was greatest during June and July when immature individuals formed the majority of both populations, thus accounting for amphipod abundance in juvenile perch stomachs in June and July (Table 8) and their abundance in adult stomachs in June (Table 9). Numbers of amphipods decreased during the remainder of the summer, fall, and winter. Biette also reported that *G. lacustris* was generally found in deeper water than *H. azteca*. *Gammarus lacustris* was usually associated with *Chara* sp. and *H. azteca* with *Potamogeton* sp.

In contrast to age 0 perch (Table 7), both juvenile and adult perch fed on a greater variety of organisms. Adult perch in particular consumed primarily insects, crayfish, and small fish. The cladoceran was never an important component in the stomachs of adult perch and only in early and late summer in the stomachs of juveniles.

SEASONAL GROWTH OF WALLEYE

Seasonal changes in growth rate of walleyes were studied by Glenn (1969) for the 1966–67 season and by Kelso and Ward (1972) for the 1969–70 season.

Glenn sampled walleye age II and older (generally larger than 25 cm total length) using nylon thread gillnets ranging in mesh size from 38.1 to 114.3 mm (stretched measure). Total and fork lengths (millimeters), and weights (grams) were recorded for captured fish. Scale samples were selected from the left side of each fish between the first and second dorsal fins immediately above the lateral line. Subsequently the scales were cleaned and impressions of scales from each fish were made on acetate plastic slides. Images of scales were projected and annuli determined. In addition, distances along anterior scale radii between the foci, annuli, and scale margins were measured and recorded. These scale and total body length measurements for 891 walleye were used to establish a body scale relation (Glenn 1969): $\hat{Y} = 51.450 + 2.023\ X$ where $\hat{Y}$ is the estimated total length of body and X is the scale measurement. The length–weight relation was $\log W = 3.163 \log L – 5.463$ (Glenn 1969) where W and L are weight (grams) and total length (millimeters).

Steps in determining seasonal growth statistics were: 1, Ages of fish were determined from the scales so that age specific growth rates could be calculated. Fish age VI and older were combined into a single group. 2, Using the scale measurement – body length relation, lengths of individual fish at annulus formation (late June 1966) were determined. 3, Weights at annulus formation were determined from the length–weight relation. Growth in both length and weight was estimated from increments between annulus formation and time of capture. 4, Average growth rates were calculated for each year-class represented in catches. 5, Seasonal growth was estimated from differences between mean growth rates of fish of known age, captured at successive sampling dates. Instantaneous daily growth rates in weight (Ricker 1958) were highest for age-groups II and III during a 3-wk period following annulus formation (Table 10). For age-groups IV and V, rates were highest during the second sampling period, i.e. between July 19 and August 2. For all age-groups rates were lower during the remainder of August and during the first 2 wk of September. Rates during fall and winter were invariably low. Instantaneous rates of growth in weight were

TABLE 10. Mean instantaneous growth rates per day in weight (grams) of walleye (*Stizostedion vitreum vitreum*) between successive sampling periods beginning at annulus formation in the 4th wk of June 1966.

Periods	Age-groups				
	II	III	IV	V	VI+
June 28–July 19	0.021	0.105	0.005	0.003	0.003
July 19 – Aug. 2	0.015	0.012	0.013	0.004	–
Aug. 2 – Aug. 26	0.002	0.004	<0.001	<0.001	<0.001
Aug. 26 – Sept. 13	0.001	0.001	0.001	0.001	<0.001
Sept. 13 – May 24	0.001	<0.001	<0.001	<0.001	<0.001

highest, as expected, for the youngest age-groups (groups II and III), and lowest for the older groups (groups V and VI+).

Ages II and III had accomplished approximately 80% of their annual increments of growth in length during the period between annulus formation and mid-September (Fig. 11A). During the same time age IV and V fish had attained between 60 and 65% of their annual total length increment. The oldest fish, 6 yr and older, had attained only 44% of their annual total by mid-September.

Growth increments in weight were more irregular (Fig. 11B). By September 13, ages II and III had attained approximately 60% of their total annual weight increments. Groups IV and V were next with about 50% of the annual total accomplished between late June and mid-September. The oldest fish again attained their annual growth more uniformly, following an initial rapid increase (Fig. 11B). By mid-September only 32% of the annual total weight increment had been attained.

Glenn (1969) concluded that the significant fall and winter weight increments in contrast with the generally minor accompanying length increments were caused by the exponential relation between length and weight. Length increases in the latter part of the growing season would produce relatively larger weight increments than similar length gains early in the season.

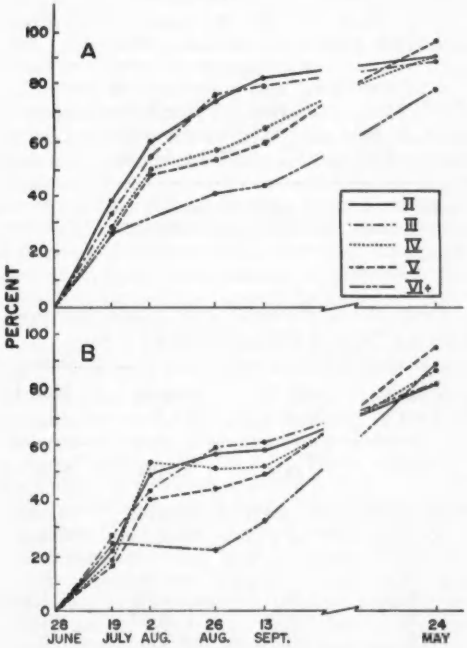


FIG. 11. Percentages of annual increments in length (A) and weight (B) attained at different times during 1966–67 by walleye of various age-groups in West Blue Lake.

During the 1969–70 growing season growth patterns were similar to those described above (Kelso and Ward 1970). In fact age III and IV walleye apparently lost weight between October 1969 and May 1970. Weight gains for age II and V fish were negligible. Kelso (1971) concluded that the majority (70–90%) of annual walleye growth was accomplished by September and virtually all (80–100%) by October 1969.

ABUNDANCE AND PRODUCTION

Walleye abundance and biomass followed a pattern related to, but not identical with, the seasonal growth pattern (Kelso and Ward 1972). The vulnerable population (i.e. fish larger than approximately 25 cm total length) increased from 1090 in May 1969 to a maximum vulnerable population of 3451 (initial surviving stock plus recruits) in October 1969 (Table 11). The population then declined during the late fall and winter to a total of 1937 in May 1970.

The difference between the two spring abundance estimates was associated with the strong year-class, age II in 1969–70. The biomass estimates in the two May periods were similar but the 1969 estimate was the larger, indicating the effect of the exponential relation between length and weight.

Production was negative between the May and June sampling periods in 1969 (Table 11). The losses were attributed to the I, II, and III age-groups (Kelso and Ward 1972).

Annual production of walleye in West Blue Lake in 1969–70 was approximately 2.8 kg ha^{-1} or 280 mg m^{-2}. Assuming that dry weight was approximately 20% of wet weight, production was 56 mg dry weight ha^{-1} and in terms of organic carbon content (450 mg C g^{-1} dry weight) 25 mg C m^{-2}. Spring–summer production (assuming 80% of annual production) was 20 mg C. Primary production approximates 35 g C m^{-2} resulting in an efficiency factor of about 0.06% between primary production and top carnivore production.

FOOD OF WALLEYE

Walleye are piscivorous or at least highly dependent on other fish as a major source of energy (Eschmeyer 1950 among many others). This dependence is also true for West Blue Lake walleye (Glenn and Ward 1968; Kelso 1973). Wet weights were determined, as described by Glenn and Ward (1968), for the various major items composing the stomach contents of 102 walleyes over 25 cm total length sampled during the summer of 1966. In all samples, excepting the June 26 collection, perch were the dominant species present (Table 12). From mid-July until mid-August, newly hatched, age 0 perch fry were a major component. They would also have been the major contribution in the August 3 sample if one walleye had not consumed one large perch.

In the late June sample, crayfish were an important diet item, and in the September sample amphipods composed a significant portion of the total wet weight of stomach contents. Insects, leeches, and other items generally made minor contributions to total stomach contents.

Assimilation efficiency in a laboratory study utilizing West Blue Lake walleye varied depending on the diet items (Kelso 1972). The efficiency for invertebrate diet items was generally lowest, 82.1% for amphipods and 83.5% for crayfish. The highest efficiencies were obtained when fish were the diet item, 96.9% for age 0 perch and 97.9% for emerald shiners. The lower assimilation efficiencies found for invertebrate foods can be attributed to the presence of indigestible exoskeletons (Kelso 1972).

Assimilation efficiency also decreased with walleye size (Kelso 1972). For example, a 200-g walleye fed a standard emerald shiner diet had an assimilation efficiency of 96.0%, whereas a 500-g fish had an efficiency of 94.6%. Although the range of values was narrow, the relation between assimilation efficiency and fish weight was significant:

TABLE 11. Estimates of abundance, biomass (B), mean biomass ($\bar{B}$), and production (P) of West Blue Lake walleye age I+ and older during the 1969–70 season (summarized and modified from Kelso and Ward 1972).

	Abundance[a]		Weights (*kg*)		
	N_1	N_2	B	$\bar{B}$	P
May 14–20, 1969	1090	*3656*	908	920	−6.26
June 16–20	1330	*3893*	931	1117	307.14
Sept. 3–12	1350	3451	1303	1069	38.41
Oct. 5–12	931	2131	834	821	1.03
May 18–22, 1970	819	1937	808		ΣP = 340.02

[a] Abundance estimates under N_1 exclude recruitment. Those under N_2 include recruitment. Italicized estimates represent potential recruits calculated from subsequent survival data.

TABLE 12. Percentage by wet weight of major food items in walleye stomachs during 1966.[a] Numerals in parentheses are the number of items. The total wet weight of stomach contents is given beneath each date.

Item	June 19 151.3 g	June 26 21.2 g	July 17 16.9 g	Aug. 3 76.60 g	Aug. 12 26.9 g	Aug. 24 217.0 g	Sept. 13 15.2 g
Amphipods	5.4(104)	0	0	0	2.0(5)	2.5(94)	31.6(180)
Perca							
0+	0	0	81.3(122)	24.2(110)	95.1(145)	3.6(26)	12.5(5)
Older	88.6(10)	18.9(1)	14.2(1)	75.8(1)	0	87.0(7)	38.2(1)
Unident. fish	1.3(4)	0	4.2(1)	0	1.9(1)	<1(1)	0
Orconectes	<1(3)	77.4(8)	0	0	0	11.8(18)	17.1(11)
Insects	1.0(19)	2.6(5)	<1	0	<1(1)	1.2(29)	<1(2)
Leeches	1.0(4)	0	0	0	<1(1)	<1(3)	0
Other	1.7(3)	<1(1)	0	0	0	2.6(2)	0

[a] The number of walleye stomachs containing food in June 19, June 26, July 17, Aug. 3, Aug. 12, Aug. 24, and Sept. 13 samples were: 24, 6, 7, 5, 14, 38, and 8.

$Y = 96.85 - 0.0045 X$ where X is walleye weight (grams) and Y is assimilation efficiency ($r = 0.91$, df 12, $P < 0.01$). Similar relations were obtained for other food items, age 0 perch and amphipods. Intercepts were different but slopes were not significantly different.

In the laboratory, fish held at temperatures less than 12 C did not grow, supporting the field data which indicated zero or negative production in late fall and winter (Table 11). Kelso also concluded that slow growth in older walleye may be related to lower assimilation efficiencies and higher metabolic demands or both. In West Blue Lake, because the walleye population is largely composed of young fish, food resources may be more efficiently utilized than in populations composed largely of older, slower growing individuals.

General Discussion

The high frequency of diatoms, flagellates, and blue-green algae in the euplankton is consistent with the flora of hardwater lakes (Prescott 1961). The spring and fall dominance of diatoms is a common occurrence (Patrick and Reimer 1966), with *Asterionella formosa* preceding *Cyclotella bodanica* during the spring bloom (Pearsall 1932).

As a means of measuring phytoplankton biomass, determination of particulate organic carbon levels in the euphotic zone of clear lakes such as West Blue Lake offers considerable advantages over both direct and other indirect procedures. The two major sources of error are the presence of small zooplankters which cannot be removed by screening and the presence of detritus. Until the contributions of detrital carbon in particular is estimated, our procedure cannot be assumed to measure phytoplankton biomass.

Our primary productivity estimates are not readily comparable with those obtained by others. Many workers have used, or are still using, Geiger-Müller preparation and counting methods. Estimates obtained by these procedures may underestimate primary productivity because "back scattering" may result in overestimates of the relative activity of ^{14}C stock solutions. Loss of ^{14}C during desiccation may also cause primary productivity to be underestimated (Ward and Nakanishi 1970), although, perhaps, the activity of desiccated algae may truly approximate net primary productivity. Losses during desiccation, particularly if the lost carbon is inorganic, therefore represent unassimilated carbon even though the carbon has passed into the cell. Alternatively, any carbon within the cell or subsequently excreted can be treated as assimilated carbon and considered as part of the photosynthetic sequence. Values for this total assimilation rate would then approximate gross photosynthetic rate.

Computation of net photosynthesis is complicated if some portion of the volatile intermediate products are normally excreted into an extracellular pool whose contents may later be available for reassimilation. A further complication arises if excreted volatile substances serve as energy sources for secondary producers, for example, bacteria. Our results are, however, comparable to values reported by Schindler and Nighswander (1970) which were not adjusted for filtration effect. Average daily primary productivity in Clear Lake for the ice-free period in 1967 was 318 mg C m^{-2}. Our estimates for approximately the same periods in 1971 and 1972 in West Blue Lake were 340 and 320 mg C m^{-2} day^{-1}, respectively.

Schindler and Holmgren (1971) report that production of extracellular carbon was generally negligible, less than 1% of light bottle fixation. This value would need to be increased, however, since their estimates of particulate productivity were increased by filtration faotors ranging from 1.2 to 6.1. In other in situ but marine experiments, Anderson and Zeutschel (1970) have estimated that extracellular productivity may be as great as 26% of particulate productivity in the euphotic zone of an oligotrophic marine station. Our estimates of West Blue Lake primary productivity are low but probably by less than their 26% maximum.

The parameters of uptake of organic acids and sugars reported here are of the same order as those reported by others (Wright and Hobbie 1965, 1966; Allen 1969). The relation between V_{max} values and bacterial numbers to six organic acids may be confirmation of the theoretical dependence of V_{max} upon population size (Hamilton et al. 1966). This relation in addition to the absence of a light effect during the 12-h incubation period is also indicative of bacterial activity rather than algal. Since bacterial activity is independent of light the daily heterotrophic production of organic carbon may well be high. This is illustrated here and our findings are consistent with the observations of Parsons and Strickland (1962) that such production may be of the same order as photosynthetic production. It should be emphasized that the reported values of heterotrophic production are of potential production. The closeness of these values to reality depend entirely upon the extent to which the added substrate may increase uptake of organic carbon. In organic acids there was no apparent proliferation of bacterial biomass during the incubation period, but nonetheless the mere presence of substrate in excess of naturally occurring amounts may render these values as overestimates.

On the other hand, however, the reported values are of net production and do not take into account possible substantial respirational loss of ^{14}C and indeed of further excreted ^{14}C organic compounds. Because of these essentially unknown effects the presented values of potential heterotrophic production must be viewed as a preliminary attempt to estimate this aspect of the energy pathways within a lake.

The influence of temperature on bacterial activity agrees with the findings of Jones (1971) who demonstrated a correlation between bacterial numbers and water temperature. However, in the relation between temperature and glucose uptake there is an assumption that plate counts more truly represent the numbers of active bacteria than would direct cell counts. We felt, however, that the alternative of utilizing direct cell counts would cause an underestimation of carbon uptake $cell^{-1}$ in excess of any overestimation that our present method may have involved.

Estimation of zooplankton production in West Blue Lake is still in the initial survey stage. We have not attempted to measure copepod productivity, and *D. pulicaria* research has been limited largely to ^{14}C uptake experiments designed to provide information on factors affecting *D. pulicaria* productivity. In general, our results indicate that the radioisotope uptake approach to estimating incorporation and eventually productivity in nature will probably be unsuccessful. There are two major difficulties. First, in situ incorporation of organic carbon is primarily controlled by the daily temperature regimes to which the animals are exposed. These regimes seem to be largely regulated in West Blue Lake, when it is thermally stratified, by the diel vertical migration patterns exhibited by the *D. pulicaria* population (Bell and Ward 1970). Diel migrations may be highly variable and quite complex. Determining migration patterns with sufficient frequency to provide reliable data to compute productivity would be onerous. Other temperature-dependent phenomena (such as egg development time, growth rates, and the duration of life history stages, used in alternative methods for estimating secondary productivity) are also affected by the daily temperature regimes experienced by the animals.

The second and more serious limitation of the isotope method relates to the complexity and variability in the composition of the living and dead particles which may serve as food for *D. pulicaria* and other zooplankters. Seasonal changes in the composition of the phytoplankton, bacterioplankton, and detritus may all affect population incorporation rates. Food preferences and particle size selectivity may make relations between biomass and incorporation rates highly variable during a season. In connection with food selectivity, incorporation rates from *Anabaena spiroides* cultures were much lower than from natural mixtures in which *A. spiroides* was a dominant species (Fig. 10). *Daphnia pulicaria* incorporation rates from cultures of bacteria occurring naturally and abundantly in West Blue Lake water are often high (Dr D. C. Gillespie, Freshwater Institute, Winnipeg, Man., personal communication) indicating that bacteria could be a significant natural food. Although our experiments and those of Schindler (1968) indicate that artificial detritus is not a good energy source for *Daphnia* sp., the inability to label natural detritus with an isotope leaves the role of natural detritus in zooplankton nutrition questionable. These difficulties require complex and unwieldy in situ experiments. Direct approaches to measuring secondary productivity based on population changes and vital statistics seem to offer more possibilities for early success.

Age 0 perch fry during summer clearly depend on *D. pulicaria* as their principal source of food. Approximately 90% of the total caloric content of age 0 perch fry during summer is in the form of *D. pulicaria* (Table 7). Translated into growth of perch, about 1.6 g of the average weight increment of an individual perch fry (1.8 g) is probably derived from feeding on *D. pulicaria*. Considering the abundance of fry in the epilimnion, as indicated by catches made by relatively brief tows with a small net (Table 6), the number of *D. pulicaria* consumed to provide energy to the age 0 perch population must have been large indeed.

The food web of older perch, juveniles, and adults is much more complex than that of age 0 fish. With relatively minor exceptions, their foods are organisms associated with the littoral zone. The components of their food web and its diversity probably indicate their requirement for energy in larger units than are needed by the fry.

Mark and release projects carried out in 1966 and 1967 indicated that the perch population is made up of units which, in the short term, do not freely intermingle. Consequently, enumeration of the total population presents problems. Furthermore, identification of annuli on scales of percholder than age II is difficult (M. R. Falk, Freshwater Institute Winnipeg, Man., personal communication). Until these problems are overcome we will not be able to measure the productivity of juvenile and adult perch.

The outstanding feature of the West Blue Lake walleye population (25 cm and longer) is that growth and production are largely confined to a brief period in summer (Table 10, 11, and Fig. 11). Furthermore, in this unfished population natural regulation of numbers took place seasonally. Minimum populations occur in spring and the maximum in late summer (Table 11). These within-year variations in production and abundance have implications for the management of commercial fisheries (Kelso and Ward 1972). If other walleye populations inhabiting large, commercially fished lakes in central Canada have seasonal growth and survival patterns similar to that of the West Blue Lake population, a fishery acting during a relatively brief period early in fall might produce optimum sustainable yields. At any rate, spring and summer fisheries for walleye seem undesirable.

Quantitative analyses of stomach contents have established a direct and significant relation between *D. pulicaria*, age 0 perch, and walleye. *Daphnia pulicaria* are the major source of energy for age 0 perch during their first summer. In turn, age 0 perch fry are apparently a major source of energy for walleye over 25 cm in total length during the summer. Stomach content data for the summer of 1966 (Table 12) indicate that age 0 perch fry formed about 29% by weight of the total stomach content of walleye in July, August, and early September. In 1969, walleye production for approximately the same period (Table 11) was 307 kg (90% of the annual total). Assuming that walleye foods and feeding were similar in both years, roughly 30% of this production was contributed by perch fry. Because about 90% of perch fry growth was apparently produced from the *D. pulicaria* population, a significant proportion of walleye annual production was probably indirectly attributable to the *D. pulicaria* population.

The role of large items in walleye nutrition, for example large perch, seems to be overemphasized by our method of treatment. A few large perch, which probably digest slowly, appearing in stomachs of only a few walleye make large contributions to total sample stomach contents, whereas smaller items more rapidly digested probably contribute at least as much to population production. Even though their role may be overemphasized, larger perch form a major fraction of the diet of walleyes.

Most groups of organisms or populations which we have studied have been treated inadequately. In addition, major components of the ecosystem have not been investigated. For example, of the benthos only the two amphipods, *Gammarus lacustris* and *Hyalella azteca* have been studied and primarily in terms of their distribution and life history (Biette 1969). Because they are an important food for perch and, to a lesser extent, for walleye, estimates of their productivity are necessary.

Current investigations at West Blue Lake are (in addition to ongoing projects, eg. measurement of primary productivity): 1, estimation of macrophyte biomass and productivity; 2, estimation of population densities and vital statistics of the *D. pulicaria* population; and 3, evaluation of introductions of walleye fry and fingerlings in the production of West Blue Lake walleye.

Acknowledgments

The following graduate students in botany or zoology at the University of Manitoba made the work at West Blue Lake both possible and worthwhile: R. K. Bell, R. M. Biette, D. D. Cliff, M. R. Falk, C. L. Glenn, L. L. Hendzel, J. R. M. Kelso, and Brian Wong. Dr N. B. Snow, a postdoctoral fellow in the Department of Zoology in 1970–71, was a stimulating colleague. Dr Snow participated in most experiments concerned with *Daphnia pulicaria* feeding. Dr D. C. Gillespie worked with us for several years in connection with bacteriological research. We appreciate his efforts and constructive criticisms. Dr K. H. Doan, Director of Research, Department of Mines, Resources, and Environmental Management and Dr H. E. Welch, Head, Department of Zoology, University of Manitoba, have both provided continuous support and valuable advice. Mr and Mrs A. Ternowski have contributed to the smooth functioning of the West Blue Lake Research Station. Undergraduate students of the University of Manitoba have worked energetically and willingly as student assistants. Financial support to F. J. Ward has been provided by the Department of Mines, Resources, and Environmental Management, and the National Research Council of Canada (A 2604). We have both received grants from the Fisheries and Marine Service to carry out research at West Blue Lake. We gratefully acknowledge the help of all these people and agencies.

ALLEN, H. L. 1969. Chemo-organo-trophic utilization of dissolved organic compounds by planktic algae and bacteria in a pond. Int. Rev. Gesamten Hydrobiol. 54: 1–33.

AMERICAN PUBLIC HEALTH ASSOCIATION, AMERICAN WATER WORKS ASSOCIATION, AND WATER POLLUTION CONTROL FEDERATION. 1965. Standard methods for the examination of water and wastewater. 11th ed. New York, N.Y. 769 p.

ANDERSON, G. C., AND R. P. ZEUTSCHEL. 1970. Release of dissolved organic matter by marine phytoplankton in coastal and offshore areas of the northeast Pacific Ocean. Limnol. Oceanogr. 15: 402–407.

ARTHUR, C. R., AND F. H. RIGLER. 1967. A possible source of error in the ^{14}C method of measuring primary productivity. Limnol. Oceanogr. 12: 121–124.

BELL, R. K., AND F. J. WARD. 1968. Use of liquid scintillation counting for measuring self-absorption of carbon-14 in *Daphnia pulex*. J. Fish. Res. Board Can. 25: 2505–2508.

1970. Incorporation of organic carbon by *Daphnia pulex*. Limnol. Oceanogr. 15: 713–726.

Biette, R. M. 1969. Life history and habitat differences between *Gammarus lacustris lacustris* Sars and *Hyalella azteca* (Saussure) in West Blue Lake, Manitoba. M.Sc. Thesis. Univ. Manitoba, Winnipeg, Man. 97 p.

Bray, G. A. 1960. A simple efficient liquid scintillator for counting aqueous solutions in a liquid scintillation counter. Anal. Biochem. 1: 279–285.

Cliff, D. D. 1972. An evaluation of a Coulter Counter method for the determination of primary productivity, and an assessment of seasonal phytoplankton biomass and species composition at West Blue Lake, Manitoba. M.Sc. Thesis. Univ. Manitoba, Winnipeg, Man. 109 p.

Davies, J. R., B. B. Bannatyne, G. S. Barry, and H. R. McCabe. 1962. Geology and mineral resources of Manitoba. Man. Mines Branch Publ. 190 p.

Eschmeyer, P. H. 1950. The life history of the walleye, *Stizostedion vitreum vitreum* (Mitchill) in Michigan. Inst. Fish. Res. Bull. No. 3: 99 p.

Falk, M. R. 1971. Food habits, gastric digestion and food consumption rates of yellow perch, *Perca fluviatilis flavescens* (Mitchill) in West Blue Lake, Manitoba. M.Sc. Thesis. Univ. Manitoba, Winnipeg, Man. 175 p.

Glenn, C. L. 1969. Seasonal rates of growth within a population of walleye, *Stizostedion vitreum vitreum* (Mitchill) in West Blue Lake, Manitoba, during 1966–1967. M.Sc. Thesis. Univ. Manitoba, Winnipeg, Man. 63 p.

Glenn, C. L., and F. J. Ward. 1968. Evaluation of "wet" weight as a field method for measuring the stomach contents of walleye, *Stizostedion vitreum vitreum* (Mitchill). J. Fish. Res. Board. Can. 25: 1505–1507.

Hamilton, R. D., K. M. Morgan, and J. D. H. Strickland. 1966. The glucose uptake kinetics of some marine bacteria. Can. J. Microbiol. 12: 995–1003.

Hendzel, L. L. 1972. The utilization of organic acids by planktonic heterotrophs in West Blue Lake, Manitoba. M.Sc. Thesis. Univ. Manitoba, Winnipeg, Man. 116 p.

Jones, J. G. 1971. Studies on freshwater bacteria: factors which influence the population and its activity. J. Ecol. 59: 593–613.

Keast, A., and L. Welsh. 1968. Daily feeding periodicities, food uptake rates and dietary changes with hour of day in some lake fishes. J. Fish. Res. Board Can. 25: 1133–1144.

Kelso, J. R. M. 1971. Population parameters and bioenergetic demands of walleye, *Stizostedion vitreum vitreum* (Mitchill) in relation to their trophic dynamic ecology, West Blue Lake, Manitoba. Ph.D. Thesis. Univ. Manitoba, Winnipeg, Man. 146 p.

1972. Conversion, maintenance, and assimilation for walleye, *Stizostedion vitreum vitreum* (Mitchill) as affected by size, diet and temperature. J. Fish. Res. Board Can. 29: 1181–1192.

1973. Seasonal energy changes in walleye and their diet in West Blue Lake, Manibota. Trans. Am. Fish. Soc. 103: 363–368.

Kelso, J. R. M., and F. J. Ward. 1972. Vital statistics, biomass, and seasonal production of an unexploited walleye (*Stizostedion vitreum vitreum* (Mitchill)) population in West Blue Lake, Manitoba. J. Fish. Res. Board Can. 29: 1043–1052.

McMahon, J. W. 1973. Membrane filter retention — a source of error in the ^{14}C method of measuring primary production. Limnol. Oceanogr. 18: 319–324.

Nalewajko, C., and D. R. S. Lean. 1972. Retention of dissolved compounds by membrane filters as an error in the ^{14}C method of primary production measurement. J. Phycol. 8: 37–43.

Narita, T., and F. J. Ward. 1972. Ingestion and incorporation by *Daphnia similis* from carbon-14 labeled *Scenedesmus* cultures. Jap. J. Limnol. 33: 36–43.

Parsons, T. R., and J. D. H. Stricland. 1962. On the production of particulate organic carbon by heterotrophic processes in sea water. Deep-Sea Res. 8: 211–222.

Patrick, R., and C. W. Reimer. 1966. The diatoms of the United States. Vol. 1. Monogr. Acad. Nat. Sci. Phila. 13: 688 p.

Pearsall, W. H. 1932. Phytoplankton in the English lakes. II. The composition of the phytoplankton in relation to dissolved substances. J. Ecol. 20: 241–262.

Prescott, G. W. 1961. Algae of the western Great Lakes area. W. C. Brown Company, Dubuque, Iowa. 977 p.

Pugh, P. R. 1970. Liquid scintillation counting of ^{14}C-diatom material on filter papers for use in productivity studies. Limnol. Oceanogr. 15: 652–655.

Ricker, W. E. 1958. Handbook of computations for biological statistics of fish populations. Bull. Fish. Res. Board Can. 119: 300 p.

Robinson, G. G. C., L. L. Hendzel, and D. C. Gillespie. 1973. A relationship between heterotrophic utilization of organic acids and bacterial populations in West Blue Lake, Manibota. Limnol. Oceanogr. 18: 264–269.

Schindler, D. W. 1968. Feeding, assimilation and respiration rates of *Daphnia magna* under various environmental conditions and their relation to production estimates. J. Anim. Ecol. 37: 369–385.

1969. Two useful devices for vertical plankton and water sampling. J. Fish. Res. Board Can. 26: 1948–1955.

Schindler, D. W., and S. K. Holmgren. 1971. Primary production and phytoplankton in the Experimental Lakes Area, northwestern Ontario, and other low carbonate waters, and a liquid scintillation method for determining ^{14}C activity in photosynthesis. J. Fish. Res. Board Can. 28: 189–201.

Schindler, D. W., and J. E. Nighswander. 1970. Nutrient supply and primary production in Clear Lake, eastern Ontario. J. Fish. Res. Board Can. 27: 2009–2036.

Schindler, D. W., R. V. Schmidt, and R. Reid. 1972. Acidification and bubbling as an alternative to filtration in determining phytoplankton production by the ^{14}C method. J. Fish. Res. Board Can. *29:* 1627–1631.

SNOW, N. B. 1972. The effect of season and animal size on the caloric content of *Daphnia pulicaria* Forbes. Limnol. Oceanogr. 17: 909–913.

SOROKIN, YU. I. 1966. Carbon-14 method in the study of the nutrition of aquatic animals. Int. Rev. Gesamten Hydrobiol. 51: 209–224.

STRICKLAND, J. D. H. 1960. Measuring the production of marine phytoplankton. Bull. Fish. Res. Board Can. 122: 173 p.

STRICKLAND, J. D. H., AND T. R. PARSONS. 1965. A manual of seawater analysis. 2nd ed. Bull. Fish. Res. Board Can. *125:* 203 p.

WALLEN, D. G., AND G. H. GEEN. 1968. Loss of radioactivity during storage of ^{14}C-labelled phytoplankton on membrane filters. J. Fish. Res. Board Can. 25: 2219–2224.

WARD, F. J., AND M. NAKANISHI. 1971. A comparison of Geiger–Müller and liquid scintillation counting methods in estimating primary productivity. Limnol. Oceanogr. 16: 560–563.

———. 1973. A comparison of liquid scintillation and Geiger–Müller estimates of primary productivity in an in situ experiment. J. Fish. Res. Board Can. 30: 708–711.

WARD, F. J., B. WONG, AND G. G. C. ROBINSON. 1970. A liquid scintillation procedure for determining the effect of size of self absorption of ^{14}C in *Daphnia pulex.* Limnol. Oceanogr. *15:* 648–652.

WEIR, T. R. 1960. Economic atlas of Manitoba. Man. Dep. Ind. Commer. Publ. 81 p.

WICKENDEN, R. T. D. 1953. Mesozoic stratigraphy of the eastern plains, Manitoba and Saskatchewan. Can. Dep. Mines Resour. 87 p.

WILLIAMS, P. J. LEB., T. BERMAN, AND O. HOLM-HANSEN. 1972. Potential sources of error in the measurement of low rates of planktonic photosynthesis and excretion. Nature 236: 91–92.

WONG, B. 1972. Growth, feeding and distribution of yellow perch fry, *Perca fluviatilis flavescens* (Mitchill), during their first summer in West Blue Lake. M.Sc. Thesis. Univ. Manitoba, Winnipeg, Man. 45 p.

WONG, B., AND F. J. WARD. 1972. Size selection of *Daphnia pulicaria* by yellow perch (*Perca flavescens*) fry in West Blue Lake, Manitoba. J. Fish. Res. Board Can. *29:* 1761–1764.

WRIGHT, R. T., AND J. E. HOBBIE. 1965. The uptake of organic solutes in lake water. Limnol. Oceanogr. 10: 22–28.

———. 1966. Use of glucose and acetate by bacteria and algae in aquatic ecosystems. Ecology 47: 447–464.

Studies of Northern Alberta Lakes and their Fish Populations[1]

M. J. PAETZ AND K. A. ZELT

Fish and Wildlife Division
Alberta Department of Lands and Forests, Edmonton, Alta.

PAETZ, M. J., AND K. A. ZELT. 1974. Studies of northern Alberta lakes and their fish populations. J. Fish. Res. Board Can. 31: 1007–1020.

The limnology and fisheries of four Alberta lakes (Cold Lake, Lac La Biche, Lesser Slave Lake, and Wabamun Lake) were described. The general description included glacial history, climate, human development, physical and chemical characteristics, plankton and macroinvertebrates, and fish species composition. Age–length relation for lake whitefish (*Coregonus clupeaformis*) and ciscoes (*C. artedii*) from the individual lakes was presented and compared with the limnological condition of the particular lake. The commercial lake whitefish yield of each lake was also compared with the physical and chemical characteristics.

PAETZ, M. J., AND K. A. ZELT. 1974. Studies of northern Alberta lakes and their fish populations. J. Fish. Res. Board Can. 31: 1007–1020.

Nous avons décrit la limnologie et les pêches de quatre lacs de l'Alberta (lac Cold, lac la Biche, Petit lac des Esclaves et lac Wabamun). La description générale a inclus histoire glaciaire, climat, développement par l'homme, caractéristiques physiques et chimiques, plancton et macroinvertébrés, et composition en espèces de poissons. Nous donnons la relation âge-longueur du grand corégone (*Coregonus clupeaformis*) et des ciscos (*C. artedii*) de chacun de ces lacs et la comparons avec les conditions limnologiques du lac en question. Nous avons comparé également, pour chacun des lacs, le rendement commercial du grand corégone avec les caractéristiques physiques et chimiques.

Accepted February 6, 1974

THE limnological characteristics of western Canadian lakes have been reviewed in broad terms by Northcote and Larkin (1963). Rawson (1947), Rawson and Atton (1951), Kennedy (1953, 1954), and Keleher (1959) have presented the results of investigations on lakes in Saskatchewan and the Northwest Territories. Miller and MacDonald (1950) and Miller and Paetz (1953) reported on a number of preliminary investigations carried out on lakes in Alberta. In recent years sufficient additional studies have been conducted in Alberta to enable us to present a more detailed picture of the limnology and the fisheries of four of the larger lakes in the province. These lakes, Lesser Slave Lake, Lac La Biche, Cold Lake, and Wabamun Lake, have been selected because of their variety of limnological characteristics and because of the relative importance of their fisheries resources to the province. Wabamun Lake is currently of particular interest because of considerable work being carried out to assess the effects of industrial warmwater discharges on the ecological system.

Geography of the Lake Drainage Basins

The four lakes lie between 53° and 55° N. lat. and between 110° and 115° W. long. The formations underlying the area are of Cretaceous and Cenozoic sedimentary origin. Wabamun Lake lies within the aspen parkland vegetative zone, whereas the other three lakes are in the boreal forest zone. According to the limnological regions of the Western Canadian Plains as outlined by Northcote and Larkin (1963), Cold Lake and Lac La Biche lie within the forest zone of freshwater lakes, and Lesser Slave and Wabamun lakes are in a transition zone between the saline lakes zone and the freshwater zone.

The lakes are located in three major drainage basins (Fig. 1). Lesser Slave Lake and Lac La Biche drain northward via the Athabasca River to the MacKenzie River. Cold Lake drains toward Hudson Bay via the Churchill River system, and Wabamun

---

[1] This paper, part of a special issue that comprises a comprehensive review of Limnology in Canada, was prepared to mark the 19th Congress of the International Association of Limnology (SIL), in Winnipeg, Man., during August 1974.

Printed in Canada (J3306)

(also Hudson Bay drainage). All these lakes are residuals of much larger glacial lakes which were formed as the Keewatin glacier retreated from the surface of the province. Lesser Slave Lake represents the southeast tip of Lake Peace; Wabamun Lake Lake lies in the North Saskatchewan watershed was part of Lake Edmonton; Lac La Biche represents the southern extremity of Lake Tyrrell; and Cold Lake is a remnant of a postglacial lake as yet unnamed.

With the exception of Cold Lake, the lakes are relatively shallow, which was also true of the glacial lakes from which they arose (Gravenor and Bayrock 1961; Taylor 1960).

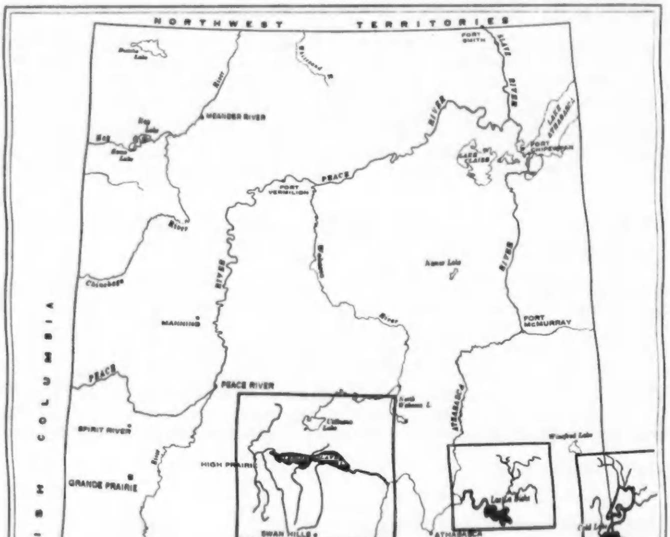

NORTHWEST TERRITORIES
BRITISH COLUMBIA
MONTANA
PROVINCE OF
ALBERTA
CANADA
ROCKY MOUNTAINS
FORT SMITH
SLAVE RIVER
LAKE ATHABASCA
FORT CHIPEWYAN
LAKE CLAIRE
MEANDER RIVER
PEACE
FORT VERMILION
MANNING
PEACE RIVER
SPIRIT RIVER
GRANDE PRAIRIE
HIGH PRAIRIE
SWAN HILLS
FORT McMURRAY
ATHABASCA
Lac La Biche
Cold Lake
COLD LAKE
WESTLOCK
ST. PAUL
WHITECOURT
Chip Lake
Wabamun L.
EDMONTON
EDSON
LLOYDMINSTER
DRAYTON VALLEY
SASKATCHEWAN
WETASKIWIN
CAMROSE
Pigeon Lake
WAINWRIGHT
JASPER
RED DEER
CORONATION
SUNDRE
DRUMHELLER
BANFF
Bow
CALGARY
RIVER
BROOKS
CLARESHOLM
SOUTH SASKATCHEWAN
MEDICINE HAT
Oldman
LETHBRIDGE
St. Mary Res.
CARDSTON
Pakowki Lake
COMPILED AND DRAWN AT THE OFFICE OF THE DIRECTOR OF SURVEYS, EDMONTON, ALBERTA, 1964

FIG. 1. Location of study lakes and their drainage basins.

The climate of the area around each of the lakes is similar, being characterized by cold winters with snow cover lasting $5\frac{1}{2}$–6 mo, and warm dry summers. On the average Cold Lake has an annual ice cover of 147 days, Wabamun Lake 172 days, Lac La Biche 179 days, and Lesser Slave Lake 199 days. The substantially shorter period of ice cover on Cold Lake is due to its greater depth, which results in slower cooling and delayed freeze-up. Spring breakup on Lac La Biche and on the main body of Wabamun Lake, west of the Wabamun power plant, occurs about 1 wk earlier than on Lesser Slave Lake and Cold Lake. A considerable portion of Wabamun Lake near the power plants remains ice free as a result of the discharge of heated effluent from the plant.

Human Developments and Land Use

Prior to settlement of the province by white settlers, the area including the four lakes was inhabited by Indians who were primarily dependent on the wildlife and fish resources for their livelihood. The Indians, being nonagricultural, did not significantly alter the land surface.

WABAMUN AREA

Since settlement, the Wabamun drainage basin has become primarily agricultural land devoted to the raising of cereal crops. In addition during the past 25 yr, much of the area immediately adjacent to the lake has been subdivided and a considerable number of summer cottages are located on the east, north, and west shores of the lake. Two coal-fired electric generating stations owned and operated by Calgary Power Limited are located adjacent to the lake — one at Wabamun on the north shore, and one at Sundance on the south shore. These plants at the present time utilize lake water for their cooling systems and discharge this water back to the lake at considerably higher than ambient temperature. Wabamun Lake is therefore being increasingly affected by the actions of man.

LESSER SLAVE AREA

The low-lying areas to the west and southwest of the lake represent portions of the former lake bed and are composed of productive agricultural soils. Cereal crop farming has been carried out for about 50 yr in the Joussard–High Prairie–Grouard triangle. This area is subject to periodic flooding by the East and West Prairie rivers, with the result that soil and nutrient materials are washed into the west basin of the lake. Lumbering was one of the chief industries in the remaining part of the drainage area until the rapid development of the petroleum industry in the Swan Hills, Mitsue Lake, and Marten Hills areas during the past decade. This development has had a dramatic effect on the watersheds along the south shore of the lake. Erosion of road ditches, seismic lines, and altered stream channels has resulted in the Swan and Driftpile rivers depositing huge amounts of soil and silt in the lake. There are seven towns or villages in the immediate vicinity of Lesser Slave Lake, and the number of mink farms (mainly on the south shore) has been as high as 220, with actual ranch mink numbers having ranged up to 106,000 animals. All of these human factors have doubtless had an effect on the lake in spite of its comparatively large size.

LAC LA BICHE

This area has been characterized by relatively sparse settlement. Two small centers of population, Plamondon and Lac La Biche are located adjacent to the lake. Agricultural activity in the drainage area is limited mainly by the nature of the soil. Some lumbering and a sizeable mink ranch industry are the remaining land use activities. The combined effects of these activities on the lake has probably been significantly less than the effects on Wabamun and Lesser Slave Lake.

COLD LAKE AREA

Cold Lake has probably been least affected of the four lakes by human land-use activities. The town of Cold Lake is the only concentration of people along the lakeshore, the remainder of the shoreline and drainage area being covered by relatively undisturbed mixed wood forest. The headwaters of the main tributary, the Martineau River, lies within the Department of National Defence Air Weapons Range. The use of air-to-surface weapons in the area, particularly on Primrose Lake in the Martineau system, has been practically the sole activity in the basin. Virtually nothing is known of the effects, if any, of such military operations on Cold Lake, except that extensive use of DDT in the past (now discontinued) has resulted in significant residues in lake trout in the lake.

Physical and Chemical Characteristics

MORPHOMETRY

The morphometry of the basins of the four lakes is shown on bathymetric charts (Fig. 2–5). Additional geographic and morphometric characteristics are presented in Table 1.

Wabamun Lake and Cold Lake, the shallowest and deepest lakes, respectively, tend to be uniform in shape, whereas the basins of both Lesser Slave Lake and Lac La Biche are divided into two parts fairly similar in area but sufficiently different in depth to create somewhat different limnological conditions in these subbasins. It is of particular limnological interest to note the relatively large volume in relation to surface area of Cold Lake as compared to the other lakes.

Although all four lakes are characterized by fluctuations in water levels, Lesser Slave Lake and Lac La Biche undergo the greatest variation in this respect (Fig. 6). Over a period of years, Lesser Slave Lake has experienced a difference of nearly 3 [illegible] between maximum and minimum levels, whereas for the same period Wabamun and Cold Lake have undergone a difference of about 1.25 m. Rather wide fluctuations in water levels could affect productivity by changing the area of the littoral zone and by changing the patterns of growth of emergent and submergent aquatic vegetation. Fishes which spawn in shallow water, such as lake whitefish (*Coregonus clupeaformis*) and northern pike (*Esox lucius*), may also be affected by exposure of spawning grounds during low water periods. Bishop (1973) suggests that low water levels are one of the factors affecting year-class strengths of ciscoes in Lesser Slave Lake.

WATER TEMPERATURE

Water temperature and rate of heating are of great importance in primary production and for

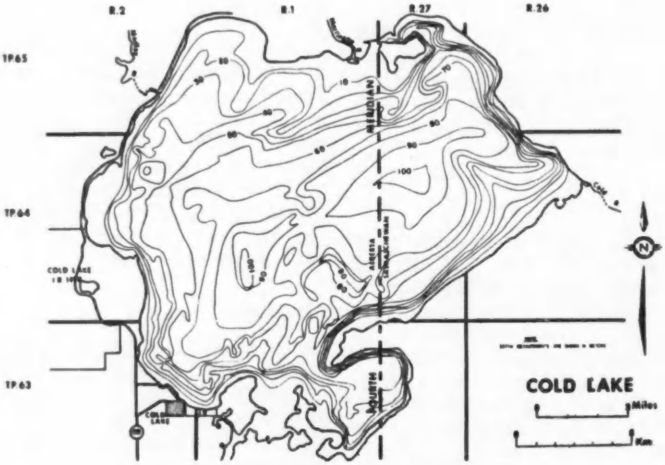


FIG. 2. Bathymetric map of Cold Lake.

TABLE 1. Location and morphometry of Cold Lake, Lac La Biche, Lake Wabamun, and Lesser Slave Lake.

	Cold Lake	Lac La Biche	Lake Wabamun	Lesser Slave Lake
Geographic coordinates				
(N. lat.)	54°33′	54°46′	53°32′	55°25′
(W. long.)	110°05′	111°58′	114°35′	115°25′
Elevation (*m*)	536.0	539.0	723.0	578.0
Surface area (*km*^{2})	372.96	229.90	82.5	1128.78
Vol (*km*^{3})	19.878	1.929	0.458	13.197
Max length (*km*)	26.90	32.2	19.3	91.3
Max width (*km*)	20.1	15.6	11.9	18.9
Mean depth (*m*)	59.7	7.4	5.4	11.7
Max depth (*m*)	100.6	22.9	11.6	19.8
Shoreline length (*km*)	105.9	161.0	57.3	241.3
Shoreline development	1.54	1.99	1.83	2.03

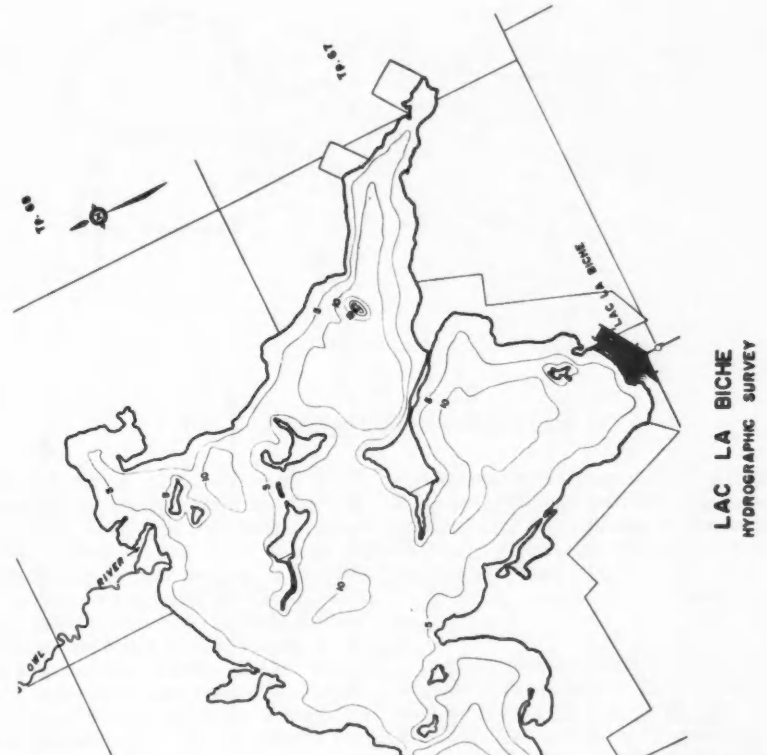

LAC LA BICHE
HYDROGRAPHIC SURVEY
NOTE:
DEPTH SHOWN IN METERS.
WEST OF 4TH MERIDIAN.
TP. 68
TP. 67
RG. 15
RG. 14
RG. 13
OWL RIVER
LA BICHE RIVER
LAC LA BICHE
LAC LA BICHE SETTLEMENT
KM
SCALE
MILES
5
10
15
20

FIG. 3. Bathymetric map of Lac La Biche.

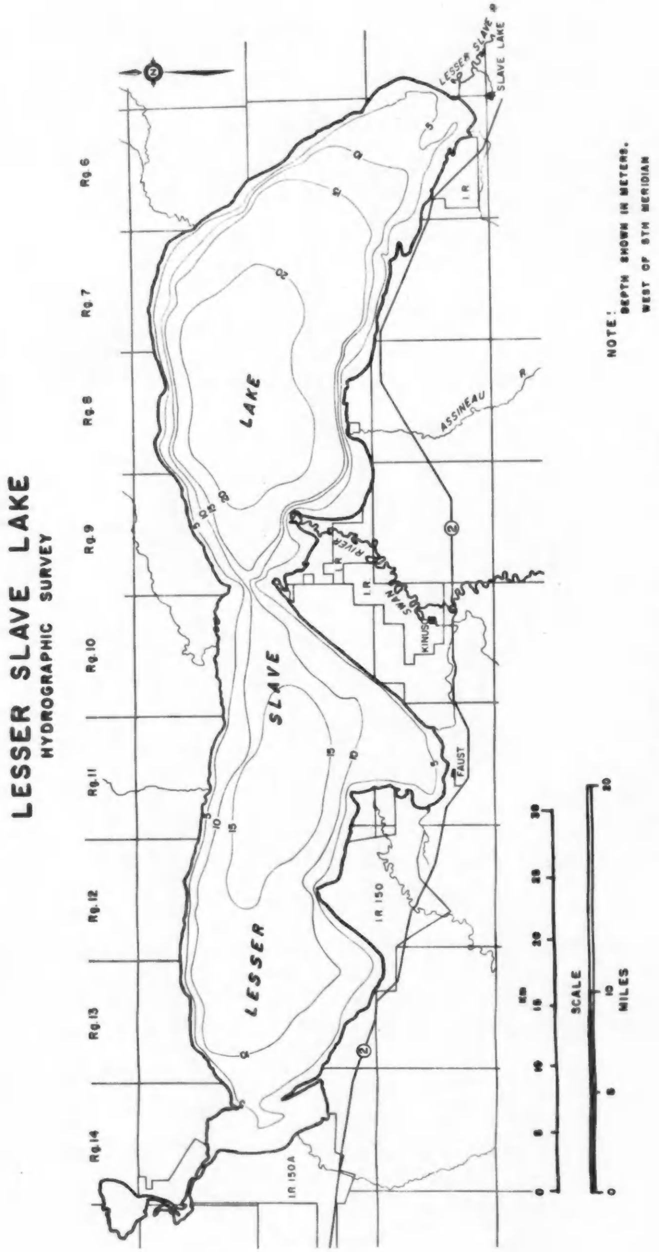

LESSER SLAVE LAKE
HYDROGRAPHIC SURVEY
Rg.6
Rg.7
Rg.8
Rg.9
Rg.10
Rg.11
Rg.12
Rg.13
Rg.14
Tp.75
Tp.74
Tp.73
LESSER
SLAVE
LAKE
SWAN RIVER
ASSINEAU R
KINUSO
FAUST
I.R
I.R 150
I.R 150A
LESSER SLAVE R
SLAVE LAKE
2
5
10
15
20
NOTE:
DEPTH SHOWN IN METERS.
WEST OF 5TH MERIDIAN
SCALE
KM
0 5 10 15 20 25 30
MILES
0 5 10 20

FIG. 4. Bathymetric map of Lesser Slave Lake.

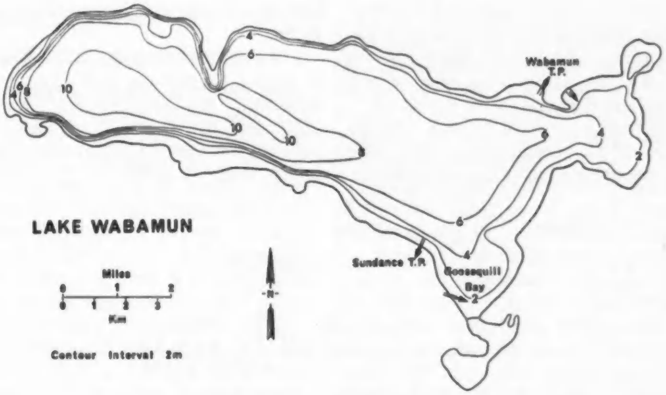


FIG. 5. Bathymetric map of Wabamun Lake.

the survival and growth of fish (Rawson 1957). Maximum surface temperature data for the four lakes provides an indication of their summer behavior with respect to this factor (Table 2). Thermal stratification is most pronounced in Cold Lake and virtually nonexistent in Lesser Slave Lake, where surface area and morphometry of the basin permit continuous mixing. Pinsent (1967) stated that summer stratification on the deeper subbasin of Lac La Biche lasts from early June to the 1st wk in September, with the thermocline generally being located from 12 to 17 m. The east subbasin of Lac La Biche does not undergo summer stratification. Prior to the establishment of the power generating stations on Wabamun Lake, thermal stratification did not become established during the summer. At present the heated discharge water forms a thin layer on the surface of the lake, creating a sharp thermocline with the underlain water of ambient lake temperature (Nursall and Gallup 1971). This sharp thermocline may be disrupted by strong winds, although stratification is reestablished with a decrease in wind velocity. This phenomenon on Wabamun Lake is almost entirely restricted to the east end of the lake. Maximum surface temperatures in this area may reach 26.5 C, whereas surface temperatures near the west end of the lake usually do not exceed 20 C (Wheelock 1969).

The thermocline in Cold Lake during July is between 9 and 15 m, and in August it is 15–21 m deep. Hypolimnetic temperatures are 4.5–8.5 C.

pH

The pH of all four lakes is alkaline (Table 2), with Lesser Slave Lake being closest to neutral and Wabamun being most alkaline (max pH 9.1). In general, the pH increases in the upper layers of these four lakes during the summer; this undoubtedly reflects the utilization of CO_2 in the trophogenic layer.

TURBIDITY

Turbidity when caused by material organic in origin is a measurement that reflects the trophic level of a lake (Ryder 1972). The low Jackson Turbidity Unit values for Cold Lake (Table 2) and the wide range exhibited by Wabamun, Lac La Biche, and Lesser Slave Lake (presumed to be due primarily to seasonal increase in biological activity) suggest that the latter are more productive.

DISSOLVED OXYGEN

Dissolved oxygen concentrations of the surface and bottom waters of the four lakes for the months of June, July, and August are presented in Table 3.

The high oxygen values in the hypolimnion of Cold Lake are indicative of its oligotrophic nature. Lac La Biche and Wabamun Lakes show some oxygen depletion in the bottom waters despite very good exposure to prevailing winds. Lesser Slave Lake circulates almost continuously throughout the summer and shows only slight oxygen depletion in the hypolimnion. Pinsent (1967) and Horkan (1971) observed winter oxygen conditions in Lac La Biche and Lake Wabamun, respectively. During the winter of 1965–66, dissolved oxygen values on Lac La Biche near the surface were 90% of saturation or greater, but those of bottom waters fell to 30% of saturation. Lake Wabamun presents a special case in that a substantial area of Kapasiwin

Bay (east end of the lake) is kept ice free. Dissolved oxygen in this area remains high (77% saturation 0.5 m above bottom on March 8, 1969) during the winter, whereas in the area of the lake subject to ice cover, dissolved oxygen fell to levels of 7 and 4% of saturation in February and March, 1969, respectively. These conditions reflect the advanced state of eutrophication of Lake Wabamun and to a somewhat lesser degree that of Lac La Biche.

Data on dissolved oxygen levels during the winter in Lesser Slave Lake and Cold Lake are lacking. However, the oligotrophic character of Cold Lake and the presence of lake trout (*Salvelinus namaycush*) would indicate minimal oxygen depletion in that body of water.

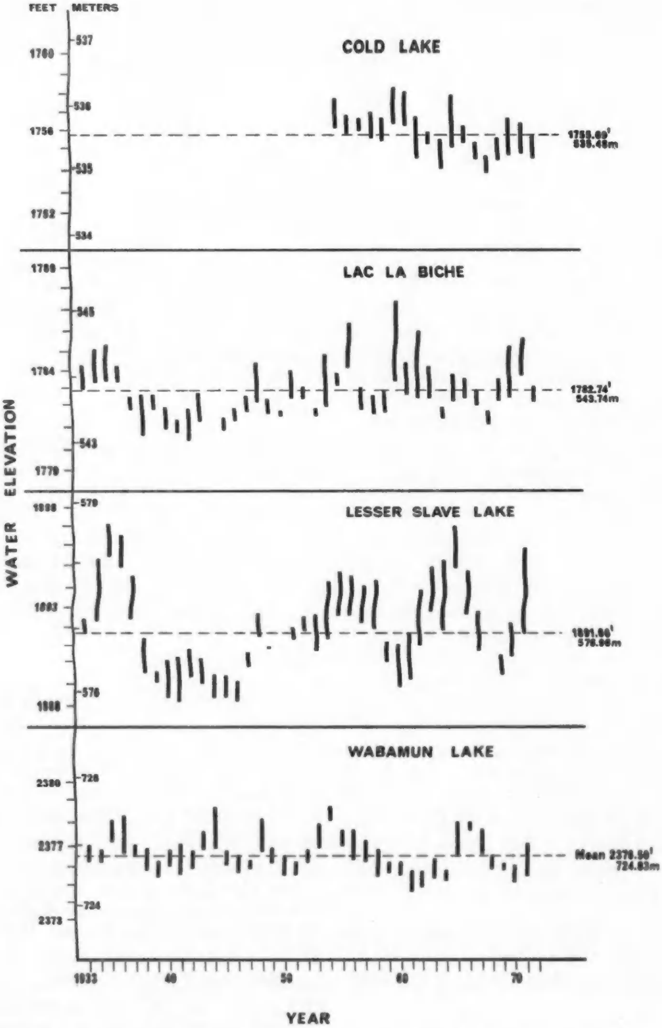


FIG. 6. Water elevations for Cold Lake, Lac La Biche, Lesser Slave Lake, and Wabamun Lake, 1933–71.

Biological Characteristics

PLANKTON AND MACROINVERTEBRATES

Comprehensive analysis (qualitative and quantitative) of plankton and bottom fauna have not been made on all four lakes. Wheelock (1969) studied phytoplankton in Wabamun Lake for the purpose of comparing the zone of heated water to the nonheated area of the lake. Maximum total phytoplankton crop occurred in August in both areas. The unheated area had 33% more cells per milliliter than the heated. Wheelock's conclusion was that the lower production in the heated water was the result of the presence of submerged macrophytes which competitively inhibited the production of phytoplankton. Furthermore, during the winter he noted that phytoplankton were present where there was no ice cover but was practically absent under ice and snow.

Using Nygaard's compound index (Nygaard 1949) and Rawson's dominant species method (Rawson 1956), Wheelock attempted to identify Wabamun Lake according to lake type using plankton. The Nygaard index indicated definite eutrophy, whereas the Rawson method indicated mesotrophy–eutrophy.

The plankton and bottom fauna communities of Lac La Biche were sampled and reported by Pinsent (1967). He illustrated the seasonal succession of dominant phytoplankton species and noted blooms of *Anabaena flos-aqua* (Lyngbye), *A. spiroides* Lemm., *Aphanizomenon flos-aqua* Lemm., *Microcyotis aeruginosa* Kuetz, and *Stephanodiscus astroea* Ehr. Pinsent points out that Lac La Biche would be eutrophic according to Hutchinson's classification of dominant limnetic algal types (Hutchinson 1967), and eutrophic–mesotrophic according to Rawson's system.

TABLE 2. Some selected physical and chemical characteristics of waters of Cold Lake, Lac La Biche, Lake Wabamun, and Lesser Slave Lake.

	Cold Lake[a]	*Lac La Biche*[b]	*Lake Wabamun*[c]	*Lesser Slave Lake*
Temp. (*C*)				
Max surface	18.2	25.7	20.4	19
Type of temp. cycle	dimictic	dimictic	dimictic	dimictic
Turbidity (JTU)	1.0–1.6	2.0–20	0–38	0–110
Secchi disc (*m*)	d	1.5–2.0	1.0–3.5	0.2–66
pH range-surface	8.1–8.6	7.4–8.8	8.2–9.1	7.0–7.4
-bottom	8.1–8.2	7.2–8.8	d	7.0–7.3
Hardness, total-surf $\bar{x}$	127	118	129	120
Total alkalinity-surf $\bar{x}$	143	141	196	210

[a] D. Gallup personal communication.
[b] M. E. Pinsent, 1967.
[c] J. M. Wheelock, 1969.
[d] Data not available.

TABLE 3. *Dissolved oxygen concentrations (ppm) of waters of Cold Lake, Lac La Biche, Lake Wabamun, and Lesser Slave Lake.*

	Cold Lake[a]		Lac La Biche[b]		Lake Wabamun[c]		Lesser Slave Lake	
	surface	bottom (74 m)	surface	bottom (19 m)	surface	bottom (9 m)	surface	bottom (15 m)
June	12.9	11.9	10.6	8.0	10.2	4.0	9.2	8.0
July	10.2	no recording	8.9	2.3	8.5	1.1	9.0	7.4
Aug.	10.1	8.0	8.6	1.0	9.5	4.8	9.5	7.0

[a] D. Gallup, 1973, personal communication.
[b] M. E. Pinsent, 1967.
[c] J. M. Wheelock, 1969.

Quantitative estimates of the standing crop of macroinvertebrates in Lac La Biche over a 2-yr period gave a value of 79.61 kg/hectare (dry weight). The decreasing order of abundance and biomass of the major groups was dipterans (Chironomidae), pelecypods, and amphipods. Quantitative estimates for the other three lakes are not available for comparison, but the values for Lac La Biche are comparable to those obtained for Big Peter Pond Lake and much greater than that of Churchill, Little Peter Pond, Ile à la Cross, and Frobisher Lakes (Rawson 1957).

The presence of the oppossum shrimp *Mysis relicta* and the amphipod *Pontoporeia affinis* in the benthos of Cold Lake and Lesser Slave Lake is noteworthy. *Mysis* has been previously recorded from deep cold lakes in the province such as Waterton Lakes, Lake Athabasca, and Leland Lakes, but not from lakes having physical and chemical features similar to those in Lesser Slave Lake. Although Lesser Slave Lake is not oligotrophic, it is still cooler than Lac La Biche and Wabamun (Table 2), and has greater depth in the east basin. These factors may have favored the survival of *Mysis*.

FISH POPULATIONS AND FISHERIES

The species of fish present in the four lakes and an estimate of their relative abundance are presented in Table 4. A total of 21 species is represented, excluding the introduced coho salmon (*Oncorhynchus kisutch*). Cold Lake, the most oligotrophic situation, contains the highest number of species (18) of the four lakes. Lesser Slave Lake contains 14 (15 at the turn of the century), Lac La Biche 13, and Wabamun (shallowest and probably most eutrophic) contains only 8 of the 21 species. For at least one species, the lake trout, it can be said that ecological conditions in two of the lakes preclude its presence. Whether lake trout were present in lakes such as Lac La Biche in earlier years is open to speculation, but apparently conditions in that lake are no longer suitable and this would also hold true for Wabamun. The lake trout has become extinct in Lesser Slave Lake since the turn of the century (personal communication with commercial fishermen), probably due to unsatisfactory ecological conditions coupled with commercial exploitation. In other words, lake trout populations in Lesser Slave Lake were dwindling naturally a century ago, and even moderate

TABLE 4. Species of fish and their relative abundance in Cold Lake, Lac La Biche, Lake Wabamun, and Lesser Slave Lake.[a]

	Cold Lake	Lac La Biche	Lesser Slave Lake	Lake Wabamun
Thymallus arcticus	-	-	+	-
Coregonus clupeaformis	+++	+++	+++	+++
Coregonus artedii	++++	++++	++++	-
Prosopium williamsoni	-	+	+	-
Salvelinus namaycush	++	-	×	-
Oncorhynchus kisutch	0	-	-	-
Esox lucius	+++	+++	+++	+++
Couesius plumbeus	+	-	-	-
Pimephales promelas	++	-	-	-
Notropis atherinoides	++	-	++	-
Notropis hudsonius	+++	+++	+++	+++
Catostomus catostomus	++	+++	++++	-
Catostomus commersoni	++	++	++	++
Lota lota	+++	+++	+++	+++
Percopsis omiscomaycus	++	++	++	-
Culaea inconstans	+	+	+	+
Pungitius pungitius	++	-	-	-
Etheostoma exile	+	+	-	+
Perca flavescens	++	++++	+++	+++
Stizostedion v. vitreum	++	++	++	-
Cottus cognatus	+	-	-	-
Cottus ricei	-	-	+	-

[a] + Rare; ++ Common; +++ Abundant; ++++ Very abundant; × Extinct; – Not present; 0 Introduced.

exploitation with the advent of commercial fishing in the early 1900s was sufficient to bring about their extinction.

Whether postglacial dispersal of species can be held strictly accountable for the paucity of species in Wabamun as compared to that of Cold Lake, or whether some have been eliminated from Wabamun, are questions that cannot be answered on the basis of evidence available at this time. However, it seems plausible to suggest that the shallow-water cisco *Coregonus artedii* is an example of a species that has not invaded the province via the Saskatchewan drainage system since the Wisconsin glaciations, and hence has not come to occupy Wabamun Lake. The longnose sucker (*Catostomus catostomus*) on the other hand is rather widely distributed in the province (Paetz and Nelson 1970), and is present in the North Saskatchewan River which has a connection with Wabamun Lake via Wabamun Creek. This suggests that this species may well have occupied the lake but has been unable to maintain itself, at least since present-day fish studies in the lake were initiated. The walleye (*Stizostedion vitreum vitreum*) is probably another example of a species which has been unable to cope with conditions in the lake for the last 50 yr or longer. This hypothesis is supported by the fact that introductions of walleye have proven to be unsuccessful.

FISH GROWTH

Comparative age-length relations for lake whitefish from Cold Lake (Allan 1973), Great Slave Lake (Bond and Turnbull 1973), Lac La Biche (Pinsent 1967), Lake Erie (Van Oosten and Hile 1947), Lesser Slave Lake (K. A. Zelt unpublished data), and Wabamun Lake (Lane 1970) are presented in Fig. 7. The growth of lake whitefish in Cold Lake, Lake Erie, Lac La Biche, and Lesser Slave Lake is similar. Slower growth rate might have been expected in Cold Lake because of oligotrophic conditions. The poor growth rate of Wabamun Lake whitefish, similar to that of Great Slave Lake, is somewhat surprising as Wabamun is the most eutrophic. Recent information would suggest that lake whitefish are abundant in Wabamun Lake, perhaps sufficiently so as to cause their present slow growth. Bidgood (1973) reported declining growth patterns in lake whitefish in Pigeon Lake coincident with high population densities.

Age-length relations for ciscoes from Cold Lake (Allan 1973), Great Slave Lake (Bond and Turnbull 1973), Lac La Biche (Robertson 1969), Lesser Slave Lake (K. A. Zelt unpublished data), and Waskesiu Lake (McLeod 1971) are compared in Fig. 8. The growth of ciscoes in Lac La Biche and Lesser Slave Lake is similar, whereas the Cold Lake ciscoes' growth is much slower. The younger ciscoes in Lac La Biche and Lesser Slave Lake are larger than those in Waskesiu Lake; however, the older ciscoes from Waskesiu Lake are larger. McLeod correlated the growth acceleration of 4-and 5-yr-old ciscoes with the increased utilization of the larval and pupal stages of certain insects

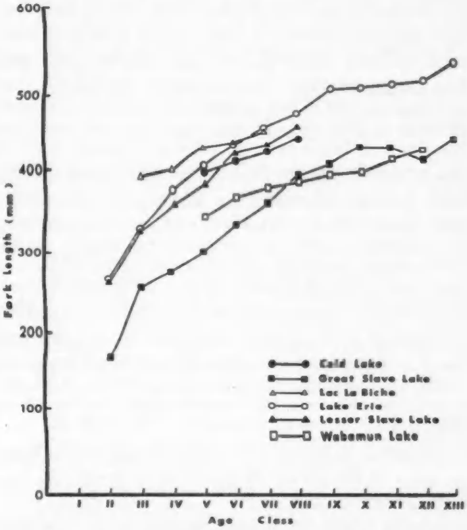


FIG. 7. Age–length relation for lake whitefish (*Coregonus clupeaformis*) from Cold Lake, Great Slave Lake, Lac La Biche, Lake Erie, Lesser Slave Lake, and Wabamun Lake.

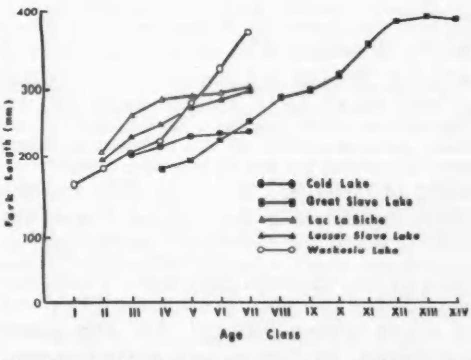


FIG. 8. Age–length relation for ciscoes (*Coregonus artedii*) from Cold Lake, Great Slave Lake, Lac La Biche, Lesser Slave Lake, and Waskesiu Lake.

and other benthic organisms. The ciscoes from Lac La Biche and Lesser Slave Lake are predominantly limnetic planktonivorous, which may account for the absence of the accelerated growth patterns.

The Commercial Fisheries

Commercial fishing licenses have been issued for fishing in Alberta at least since as early as 1910. Domestic fishing with gillnets probably began before that date. Limitations in the catch of certain species, such as lake whitefish in Lesser Slave Lake and Lac La Biche, have been in effect since 1917. No reliable records of the number of commercial fishing licenses or the annual catch appear to be available for the four lakes prior to 1930. For the past 30 yr the principle species taken by commercial fishing have been as follows: Lake Wabamun, lake whitefish; Lac La Biche, lake whitefish, ciscoes, walleye, and northern pike; Lesser Slave Lake, lake whitefish, ciscoes, walleye, and northern pike; and Cold Lake, lake whitefish, lake trout, and recently ciscoes. Lake whitefish have been the most important species in terms of value. Ciscoes in Lesser Slave Lake and Lac La Biche have been heavily exploited for mink food. The annual commercial production of whitefish from the four lakes since 1942 is shown in Table 5.

Whitefish fisheries in Alberta have been subject to wide fluctuations. Miller (1956) attributes the failure of the fisheries to weak year-classes, the causes of which have been subject to considerable investigation elsewhere but are still not clearly understood. The whitefish fisheries of the four lakes under consideration have been subject to these fluctuations (Table 5). The Lake Wabamun commercial fishery collapsed in 1961–62 after attaining a yield of slightly over 450,000 kg 6 yr earlier. The Lesser Slave Lake whitefish fishery had to be closed in 1965–66 due to a scarcity of whitefish. This lake had also produced an average of over 450,000 kg for the 5-yr period 1958–62. The recovery of this particular fishery has been very slow. After a closure of the commercial fishery for 5 yr annual production now has reached only about 68,000 kg/yr. The Lac La Biche whitefish fishery experienced a sharp decline between the 1958–62 period and the 1963–67 period, and production was also low in three consecutive periods prior to 1958. The Cold Lake fishery is somewhat more difficult to analyze, due to the lengthy period of closure between 1948 and 1955. This closure was designed to allow recovery of the lake trout population, which had virtually collapsed probably due to overexploitation. It is known, however, that in individual years of high yield, commercial whitefish production in Cold Lake has been 25 times greater than that of years of lowest yield.

Current management practices on the four lakes entail the setting of lower annual commercial whitefish quotas than were previously allowed (i.e. more moderate rates of exploitation). An annual quota of 45,000 kg on Cold Lake for the past 10 yr, for example, has thus far resulted in a more stable whitefish year-class structure.

Sport Fisheries

The two lakes which have attracted the interest of sport fishermen have been Cold Lake, primarily because of the presence of lake trout, and Wabamun Lake, due to its proximity to the City of Edmonton.

TABLE 5. Annual commercial catch (kilograms) of lake whitefish (*Coregonus clupeaformis*) from Cold Lake, Lac La Biche, Lesser Slave Lake, and Wabamun Lake for the period 1942–72.

Year	Cold Lake	Lac La Biche	Lesser Slave Lake	Wabamun Lake
1942	139,778	55,662	115,039	Closed
1943	97,809	35,154	108,143	Closed
1944	117,813	4,416	131,075	141,335
1945	144,240	818	162,179	153,497
1946	61,171	244	119,195	241,667
1947	43,722	2,057	102,246	167,430
1948	Closed	Closed	202,702	136,320
1949	Closed	Closed	259,384	125,925
1950	Closed	4,393	310,145	136,259
1951	Closed	34,270	431,354	112,745
1952	Closed	56,130	482,912	62,889
1953	Closed	49,414	516,551	90,217
1954	Closed	1,127	404,008	183,010
1955	65,458	26,774	212,910	478,998
1956	233,802	50,318	183,240	204,909
1957	68,040	129,619	373,216	151,544
1958	166,084	240,102	404,539	113,526
1959	80,877	262,811	445,552	55,080
1960	138,501	353,328	636,486	57,330
1961	47,915	85,796	436,831	Closed
1962	24,098	31,218	275,334	1,442
1963	54,940	32,475	205,225	3,205
1964	9,193	97,695	46,668	Closed
1965	42,890	89,697	Closed	40,824
1966	41,233	79,303	Closed	10,433
1967	57,665	81,910	Closed	23,633
1968	43,829	96,510	Closed	20,716
1969	45,341	77,154	44,180	25,355
1970	34,998	71,822	36,444	18,154
1971	45,201	71,524	29,607	23,976
1972	27,800	66,345	70,041	47,810

It is estimated (Lane 1970) that a total of 44,000 man-days of angling per year are spent on Wabamun Lake, resulting in a harvest of approximately 30,000 kg of pike and 63,000 kg of lake whitefish. Lake Wabamun is one of the few lakes in the province on which a significant sport fishery for lake whitefish has developed. It is probably the most active winter sport fishery in the province at the present time.

The continuing low population level of lake trout in Cold Lake following the virtual collapse of the fishery in the late 1940s has resulted in a low sport fishing effort but a sustained high degree of interest on the part of anglers. A 3-yr experiment involving the introduction of coho salmon in the lake (1970–72) did not result in establishing a sport fishery for this species. Success was far short of that experiment in the Great Lakes with the same species, and the data are now being analyzed to determine the reasons for the failure.

The sport fishery potential of Lesser Slave Lake and Lac La Biche, largely in pike, walleye, and perch, is not being exploited to any significant degree. The size of these lakes and the fact that they are subject to storms are the main reasons for the lack of effort on the part of sport fishermen. They are expected to play a more important role in this regard as human populations and angler demands increase.

Discussion

On the basis of mean depth, turbidity, oxygen, and water temperature, the four lakes can be broadly placed into an oligotrophic–mesotrophic–eutrophic classification. Cold Lake is oligotrophic whereas Wabamun Lake is eutrophic. Lesser Slave Lake and Lac La Biche exhibit an intermediate condition (mesotrophic). Analysis of phytoplankton in two of the lakes, Wabamun and Lac La Biche, support this contention. In further examining the biological productivity with reference to lake whitefish yields, the same relative order of productivity can be established. If one calculates the average commercial lake whitefish production for a 10-yr period during which individual lakes have been consecutively harvested, it is found that Cold Lake yielded 2.38 kg/hectare, Lesser Slave Lake 3.62 kg/hectare, Lac La Biche 5.69 kg/hectare, and Wabamun Lake 20.12 kg/hectare. These rates of exploitation, although consistent with the expected order of productivity, probably exceeded the sustainable yield because collapses in the lake whitefish fisheries were observed. To more effectively manage these fish populations, it will be necessary to understand in more detail the relation of abiotic factors to biological productivity. This is particularly urgent in situations where the activities of man are altering the ecosystem, as is already exemplified on Wabamun Lake.

Allan, J. H. 1973. The whitefish fishery of Cold Lake. Alta. Dep. Lands For. Fish. Branch. 12 p. (unpublished report)

Bidgood, B. F. 1973. Divergent growth in two lake whitefish (*Coregonus clupeaformis*) populations. J. Fish. Res. Board Can. 30: 1683–1696.

Bishop, F. G. 1973. A theory to explain population fluctuations of cisco in Lesser Slave Lake. Alta. Dep. Lands For. Fish. Branch. 11 p. (unpublished report)

Bond, W. A., and T. D. Turnbull. 1973. Fishery investigations at Great Slave Lake, Northwest Territories 1972. Dep. Environ. Tech. Rep. No. CEN/T-73-7: 78 p.

Gravenor, C. P., and L. A. Bayrock. 1961. Glacial deposits of Alberta. R. Soc. Can. Publ. 3: 33–50.

Horkan, J. P. K. 1971. Some ecological effects of thermal pollution on Lake Wabamun, with special reference to the Rotifera. M.Sc. Thesis. Univ. Alberta, Edmonton, Alta. 168 p.

Hutchinson, G. E. 1967. A treatise on limnology. Vol. II. Wiley and Sons, New York, N.Y. 1015 p.

Keleher, J. J. 1959. Fisheries research at Great Slave Lake. Fish. Res. Board Can. Biol. Sta. Technol. Unit. (London) Prog. Rep. 1: 41–44.

Kennedy, W. A. 1953. Growth, maturity, fecundity and mortality in the relatively unexploited whitefish, *Coregonus clupeaformis*, of Great Slave Lake. J. Fish. Res. Board Can. 10: 413–441.

1954. Growth, maturity and mortality in the relatively unexploited lake trout, *Cristivomer namaycush*, of Great Slave Lake. J. Fish. Res. Board Can. 11: 827–852.

Lane, C. B. 1970. A six month creel survey of Wabamun Lake, Alberta, 1968–69. Alta. Dep. Lands For. Manage. Rep. No. 12: 35 p.

McLeod, C. L. 1971. Food and feeding habits of the cisco, *Coregonus* (Leucichthys) *artedii*, in Waskesiu Lake, Prince Albert National Park, Saskatchewan. M.Sc. Thesis. Univ. Calgary, Calgary, Alta. 103 p.

Miller, R. B. 1956. The collapse and recovery of a small whitefish fishery. J. Fish. Res. Board Can. 13: 135–146.

Miller, R. B., and W. H. MacDonald. 1950. Preliminary biological surveys of Alberta watersheds, 1947–1949. Alta. Dep. Lands For. 139 p.

Miller, R. B., and M. J. Paetz. 1953. Preliminary biological surveys of Alberta watersheds, 1950–52. Alta. Dep. Lands For. 114 p.

Northcote, T. G., and P. A. Larkin. 1963. Western Canada, p. 451–485. *In* D. G. Frey [ed.] Limnology in North America. The University of Wisconsin Press., Madison, Wis.

Nursall, J. R., and D. N. Gallup. 1971. The responses of the biota of Lake Wabamun, Alberta, to thermal effluent, p. 295–304. *In* Proc. International Symp. on the Identification and Measurement of Environmental Pollutants, Ottawa.

NYGAARD, G. 1949. Hydrobiological studies in some ponds and lakes. Part 2. The quotient hypothesis and some new or little known phytoplankton organisms. K. Danske. Vidensk. Selsk. Biol. Skr. 7: 1–293.

PAETZ, M. J., AND J. S. NELSON. 1970. The fishes of Alberta. The Queen's Printer, Edmonton, Alta. 281 p.

PINSENT, M. E. 1967. A comparative limnological study of Lac La Biche and Beaver Lake, Alberta. M.Sc. Thesis. Univ. Alberta, Edmonton, Alta. 147 p.

RAWSON, D. S. 1947. Lake Athabasca. Bull. Fish Res. Board Can. 72: 69–85.

1956. Algal indicators of trophic lake types. Limnol. Oceanogr. 1: 18–25.

1957. Limnology and fisheries of five lakes in the upper Churchill drainage, Saskatchewan. Sask. Dep. Nat. Resour. Fish. Branch Rep. 3: 61 p.

RAWSON, D. S., AND F. M. ATTON. 1951. Fisheries investigations of Lac La Ronge, Saskatchewan, 1948, 1949. Sask. Dep. Nat. Resour. Fish. Branch. 117 p. (unpublished report)

ROBERTSON, M. R. 1969. The cisco fishery of Lac La Biche. Alta. Dep. Lands For. Manage. Rep. No. 9: 10 p.

RYDER, R. A. 1972. The limnology and fishes of oligotrophic glacial lakes in North America (about 1800 A.D.). J. Fish. Res. Board Can. 29: 617–628.

TAYLOR, R. S. 1960. Some pleistocene lakes of northern Alberta and adjacent areas (revised). J. Alta. Soc. Pet. Geol. 6: 167–185.

VAN OOSTEN, J., AND R. HILE. 1947. Age and growth of the lake whitefish, *Coregonus clupeaformis* (Mitchill), in Lake Erie. Trans. Am. Fish. Soc. 77: 178–249.

WHEELOCK, J. M. 1969. Phytoplankton ecology in Wabamun Lake and the effect of thermal pollution. M.Sc. Thesis. Univ. Alberta, Edmonton, Alta. 178 p.

Coming Next Month/ A paraître le mois prochain

Abundance and potential pathology of parasites infecting salmonids in Canadian Maritime hatcheries **G. M. Hare and C. Frantsi**

Seasonal distributions of bottom fishes in the Narragansett Bay area: seven-year variations in the abundance of winter flounder (*Pseudopleuronectes americanus*) **H. P. Jeffries and W. C. Johnson**

A digital echo-counting system used in determining abundance of freshwater pelagic fish in relation to depth **J. R. M. Kelso and E. E. Pickett**

Liver fat and protein metabolism in rainbow trout (*Salmo gairdneri*) fed cyclopropenoid fatty acids **Y. Malevski, M. W. Montgomery, and R. O. Sinnhuber**

Growth stimulation and biochemical changes in juvenile coho salmon (*Oncorhynchus nerka*) exposed to bleached kraft pulpmill effluent for 200 days **D. J. McLeay and D. A. Brown**

Olfactory response and fenitrothion toxicity in American lobsters (*Homarus americanus*) **D. W. McLeese**

Plankton, chemistry, and physics of lakes in the Churchill Falls region of Labrador **H. C. Duthie and M. L. Ostrofsky**

Migrations and intermingling of Atlantic cod (*Gadus morhua*) stocks of the Newfoundland area **W. Templeman**

Descriptions of a new species of *Barathronus* (Pisces, Aphyonidae) and four specimens of *Sciadonus* sp. from the eastern Pacific **J. G. Nielsen and R. Eagle**

In vitro phagocytosis by hemocytes of the American lobster (*Homarus americanus*) **W. D. Paterson and J. E. Stewart**

Transferrin variation in North American populations of the Atlantic salmon (*Salmo salar*) **R. H. Payne**

Composition, processing, and utilization of red crab (*Pleuroncodes planipes*) as an aquacultural feed ingredient **J. Spinelli, L. Lehman, and D. Wieg**

Notes

Adjustment of buoyancy and excess internal pressure of swimbladder gases in some North American freshwater fishes **J. H. Gee, K. Machniak, and S. M. Chalanchuk**

Parasites of freshwater and anadromous fishes from Matamek River system, Quebec **G. Hanek and K. Molnar**

Fluoride concentrations in two Pacific coast inlets — an indication of industrial contamination **R. M. Harbo, F. T. McComas, and J. A. J. Thompson**

Natural mortality rate in last winter of life of coho salmon (*Oncorhynchus kisutch*) resident in Puget Sound **S. B. Mathews and R. Buckley**

Properties of age structure models for fish populations **R. L. Allen and P. Basasibwaki**

Functionality of fish muscle: emulsification capacity **E. A. Childs**

Meristic variation in the threespine stickleback, *Gasterosteus aculeatus*, in the Matamek River system, Quebec **B. W. Coad and G. Power**

Effects of water salinity and dietary protein levels on total serum protein and hematocrit of rainbow trout (*Salmo gairdneri*) fingerlings **I. H. Zeitoun, D. E. Ullrey, and P. I. Tack**

Influence of salinity on protein requirements of coho salmon (*Oncorhynchus kisutch*) smolts **I. H. Zeitoun, D. E. Ullrey, J. E. Halver, P. I. Tack, and W. T. Magee**

Swimming depth of adult American eels (*Anguilla rostrata*) in a saltwater bay as determined by ultrasonic tracking **A. B. Stasko and S. A. Rommel Jr.**

A syringe volumetric measuring device **G. L. Myers and J. J. Peterka**

Journal
Fisheries
Research
Board
Canada

Guide to Authors

A more detailed guide on preparation of manuscripts from theses is available from the Office of the Editor.

EDITORIAL PRACTICES

The *Style Manual for Biological Journals* (3rd ed. American Institute of Biological Sciences, 3900 Wisconsin Ave. NW., Washington, D.C.) is used as the authority in matters of form. The standards for spelling are: *Webster's Third New International Dictionary* and *le Grand Larousse Encyclopédique*. Titles of periodicals are abbreviated as in the *Biological Abstracts* list. References to literature are made by the name-and-year system. The *Journal* follows the names and spelling recommended in *A List of Common and Scientific Names of Fishes from the United States and Canada* (Third Edition, 1970), Special Publication No. 6 of the American Fisheries Society.

Notes are distinguished from *papers* on the basis of scope or completeness, rather than quality, of the research. They may be on problems with narrow, readily defined limits; on work that is largely confirmatory; on fishing gear or methods, or research techniques; on advances in knowledge arising as by-products of broader studies; on progress in projects that were discontinued; or on preliminary findings that warrant publication before problems are resolved. They may be organized with as much flexibility as papers except that they may have no centered headings. They should take no more than four pages in the *Journal*.

Series titles should be avoided. An *abstract* is required. Authors are encouraged to submit abstracts in both English and French; those submitted in one language only are translated by the *Journal*.

Line drawings are preferably made with black india ink on white drawing or tracing paper or on coordinate paper with blue grids. All lines, symbols, letters, and numerals must be neat, and at least 1 mm high when the illustration is reduced to the appropriate size. Drawings should be grouped to facilitate comparisons. Originals must be submitted and should be less than 50 cm in the greater dimension for full-page illustrations, and proportionately smaller for those taking less than a page. Drawings must not be rolled for mailing.

Photographs should be printed on glossy paper with a wide range in tone. They should be cropped, squared, and mounted on white cardboard, with no spaces between those arranged in groups.

Galley proof is sent to the author, and he is responsible for detecting errors in printing as well as in content.

Fifty *reprints*, without covers, are supplied free. Additional copies may be ordered when the galley proof is returned. A charge of $30.00 per page is made for articles published. When submitting a manuscript, an author should state that his institution will accept this charge.

CHECKLIST ON MANUSCRIPTS

Attention to the following questions will expedite appraisal of manuscripts by referees and editors.

Are the findings, interpretations, and conclusions adequately documented and relevant to the purpose of the study?

Are all the tables and figures needed, and organized to facilitate comparisons? Are there inconsistencies between tables or figures and the text, or within the text? Should some of the data be made available separately, in a manuscript report or at a data repository? If you use statistical analysis are the statistics subordinate to the biology?

Would any of the text be clearer if condensed? Are summary statements given at the beginnings of sections and paragraphs, and are details in sections and paragraphs relevant to their topics? Does the organization of the manuscript follow logically from the statement of purpose in the introduction?

Does the *title* encompass the content of the report?

Does the *abstract* give the essentials of the new knowledge?

Is the *introduction* largely limited to the scope, purpose, and rationale of the study? Is review of the literature limited to defining the problem?

Are details of *materials and methods* limited to what scientists need in understanding the design of the study and in judging adequacy of the data?

Are generalizations on the *results* adequate? Are findings distinguished from inferences from them?

Is *discussion* limited to interpretation and significance of the findings?

Journal
Fisheries
Research
Board
Canada

Guide des Auteurs

On peut se procurer au bureau du Directeur de la publication un guide plus détaillé pour la préparation de manuscrits à partir de thèses.

DISPOSITIONS GÉNÉRALES

Le *Style Manual for Biological Journals* (3e éd., publié par l'American Institute of Biological Sciences, 3900 avenue Wisconsin N.O., Washington, D.C.) sert de guide quant à la forme de présentation. Le *Webster's Third New International Dictionary* et le *Grand Larousse Encyclopédique* font autorité pour l'orthographe des mots. Les titres de périodiques sont abrégés suivant les *Biological Abstracts*. Les références bibliographiques dans le texte doivent suivre le système nom de l'auteur-année. Pour les noms de poissons et leur orthographe, le *Journal* suit les recommandations contenues dans *A List of Common and Scientific Names of Fishes from the United States and Canada* (Troisième édition, 1970), Publication spéciale No. 6 de l'American Fisheries Society.

Les *notes* se distinguent des *articles* par la portée et le degré d'achèvement, plutôt que par la qualité des recherches. Les notes peuvent traiter de problèmes à portée restreinte et facilement définissables; de travaux qui en corroborent d'autres; d'engins et de méthodes de pêche, ou de techniques de recherche; de découvertes dérivées d'une recherche de plus grande envergure; de progrès accomplis dans l'exécution de projets abandonnés; enfin, de résultats préliminaires assez importants pour en justifier la publication avant la solution complète du problème. L'agencement des notes peut être aussi flexible que celui des articles, sauf qu'elles ne doivent pas avoir d'en-têtes de paragraphes centrés. La longueur ne doit pas dépasser quatre pages.

On doit en général éviter les *titres en séries*. L'auteur doit fournir un *résumé*. Si possible, le résumé devra être produit en anglais et en français; le *Journal* se charge de la traduction des résumés soumis en une seule langue.

Les *dessins au trait* doivent être éxécutés de préférence à l'encre de Chine sur papier à dessin blanc, sur papier à calquer ou sur papier quadrillé bleu. Lignes, symboles, lettres et chiffres doivent être soignés et mesurer au moins 1 mm de hauteur lorsque la figure est réduite à la dimension voulue. On groupera les dessins de façon à faciliter les comparaisons. Les dessins originaux doivent accompagner le manuscrit, et ne doivent pas dépasser 50 cm dans le sens le plus long s'ils représentent une figure devant couvrir une page entière; ils seront proportionnellement plus petits pour des figures de moins d'une page. Les dessins doivent être postés à plat.

Les épreuves de *photographies* doivent être tirées sur papier glacé à gamme de ton étendue. Elles doivent être coupées, dressées et montées sur carton blanc, sans laisser d'espace entre celles qui sont disposées par groupes.

Les *épreuves en placards* sont adressées à l'auteur et il lui incombe de corriger toute erreur d'impression ou de contenu.

Cinquante *tirés à part*, sans couverture, sont fournis gratuitement. L'auteur peut profiter du renvoi des épreuves en placards pour commander des tirés à part supplémentaires. Les frais sont de $30.00 par page pour la publication des articles. Quand un auteur soumet un manuscrit, il doit spécifier que son institution accepte les frais.

LISTE DE CONTRÔLES POUR MANUSCRITS

Une attention particulière aux questions suivantes facilitera l'évaluation des manuscrits par les arbitres et les éditeurs.

Les découvertes, interprétations et conclusions sont-elles bien documentées et pertinentes au but de l'étude?

Les tableaux et figures sont-ils tous nécessaires et agencés pour faciliter les comparaisons? Y a-t-il contradiction entre les tableaux ou les figures et le texte, ou dans le texte même? Est-ce que certaines données devraient être présentées séparément, dans un rapport manuscrit ou dans un dépôt de données? Si vous faites une analyse statistique, la statistique cède-t-elle le pas à la biologie?

Le texte y gagnerait-il en clarté s'il était plus condensé, en tout ou en partie? Contient-il des exposés sommaires *au début de chaque section ou paragraphe, et les détails* de ces sections et paragraphes sont-ils pertinents au sujet traité? La marche du manuscrit est-elle conforme à la logique énoncée dans l'introduction?

Le *titre* est-il concis, tout en étant représentatif du contenu du rapport?

Le *résumé* donne-t-il l'essentiel des connaissances nouvelles?

L'*introduction* se limite-t-elle à une esquisse de la portée, du but et des raisons de l'étude? La revue de la littérature se limite-t-elle à la définition du problème?

La section *matériel et méthode* contient-elle le minimum de détails qui permettront aux autres scientifiques de saisir les grandes lignes de l'étude et de juger de la valeur des données?

Les généralisations sur les *résultats* sont-elles adéquates? Permettent-elles de distinguer entre constatations et déductions?

La *discussion* est-elle limitée à l'interprétation et à l'évaluation des découvertes?

Journal
Fisheries
Research
Board
Canada

Guide for Typists Preparing Copy

Read "Guide to Authors" in the current volume of the *Journal*. When in doubt about how to type or arrange details, follow *Journal* practice.

Type the manuscript on white bond paper, not flimsy, preferably size 21.5 × 28 cm (8.5 × 11 inches). If possible, use paper with the lines numbered in the margin. *Leave all margins at least 2.5 cm wide.*

Double-space all parts of the manuscript, including tables, captions for illustrations, footnotes, and the reference list. Underline only material that is to be printed in italics. Indent the first line of each paragraph in the text and of each footnote.

In titles and headings, capitalize only the first word and proper names and adjectives. For small capitals, use small letters.

Indicate all text footnotes by superscript arabic numerals. Number them consecutively throughout the manuscript, starting with those on the title page. Place each footnote immediately below the reference to it, separating it from the text by horizontal lines.

On the first page type only the title, the authors' names and affiliations, related footnotes, and the running head (see Appendix A). Type the abstract on a separate page (see Appendix B). Number all pages, beginning with the title page and including those for tables and captions for illustrations.

Have the author check the finished manuscript, and send the ribbon copy and another clear copy to the Office of the Editor.

Tables: Examine the current volume of the *Journal* to see how tables are set up (see Appendix C). Note especially the following concerning *numbered tables:*

Type each on a separate page, using paper without the lines numbered.

Number them with arabic numerals.

Use horizontal lines above and below the headings and below the columns, and seldom elsewhere. Never use vertical lines; leave extra spaces instead.

Indicate table footnotes by superscript small letters *and type them below the table.*

Place the tables after the list of references.

Where each table is first referred to, type in the margin "Table — near here."

Note that *text tables* are not numbered, are typed with the text, and seldom need horizontal lines (see Appendix C).

Illustrations: Send the *original* and two clear copies of each illustration with the manuscript. At the lower left of each figure and copy, give the author's name and the figure number. Also, type each caption with its figure *for identification. For photographs, type this information* on a strip of paper and fasten it to the back of the print. Do not write or type on the print itself. Also, type the captions in succession on a separate page, headed "Captions for illustrations." Put this page at the end of the manuscript.

Where each figure is first referred to, type in the margin "Fig. — near here."

Mathematical Expressions, Equations, and Formulas: Leave three spaces above and below lines that have much material in superscripts, and above and below equations and formulas. In the various expressions, place each component in its correct position (see Appendix D).

Show all symbols clearly. In the margin, spell out Greek letters the first time they occur, and distinguish between the small letter l and the numeral *one*, and between the capital letter O and the numeral *zero*. Make *other explanatory notes similarly.*

References: Check the text to see that all references in the list are referred to. Type the reference list, double-spaced, in the style used in the *Journal* (see Appendix E). Names of journals are abbreviated as in the *Biological Abstracts* list; if an abbreviation is in doubt, type the name in full.

Spellings: About 100 words common in fisheries journals are listed in Appendix F.

Appendices: Appendices A to F are available on request from the Office of the Editor.

Journal
Fisheries
Research
Board
Canada

Guide pour les secrétaires d'auteurs

Lisez le "Guide des Auteurs" reproduit dans l'édition courante du *Journal*. Si vous avez des doutes sur la façon de dactylographier le texte ou d'en agencer les détails, suivez la pratique du *Journal*.

Dactylographiez le manuscrit sur papier blanc de bonne qualité, et non sur papier pelure, mesurant de préférence 21.5 × 28 cm (8.5 × 11 pouces), laissant toujours une marge d'au moins 2.5 cm. Si possible, employez un papier avec lignes numérotées en marge.

Tout le manuscrit, y compris tableaux, légendes de figures, renvois et références bibliographiques, devra être dactylographié à double interligne. Ne soulignez que les mots qui devront être imprimés en italique. Mettez en retrait la première ligne de chaque paragraphe du texte et de chaque renvoi.

Dans les titres et les en-têtes, n'employez la majuscule que pour le premier mot et les noms propres. Pour les petites majuscules, employez les minuscules du dactylographe.

Indiquez tous les renvois du texte par des chiffres arabes suscrits. Numérotez les renvois consécutivement par tout le texte, à commencer par ceux de la page titre. Placez chaque renvoi directement sous sa référence, le séparant du texte par des lignes horizontales.

La première page ne doit contenir que le titre de la publication, le nom et l'affiliation de ou des auteurs, les renvois appropriés et le titre courant (voir Appendice A). Dactylographiez le résumé sur une page séparée (voir Appendice B). Numérotez chaque page, à commencer par la page titre, et y compris celles qui contiennent les tableaux et la légende des figures.

Voyez à ce que l'auteur vérifie le manuscrit final, et soumettez la première copie et une seconde copie suffisamment claire au bureau du Directeur de la publication.

Tableaux: Consultez une copie du *Journal* pour la composition des tableaux (voir Appendice C). Portez une attention particulière à ce qui suit au sujet des *tableaux numérotés*.

Dactylographiez chaque tableau sur feuille séparée, vous servant de papier sans lignes numérotées.

Numérotez les tableaux en chiffres arabes.

Tracez des lignes horizontales au-dessus et au-dessous des en-têtes et au-dessous des colonnes, rarement ailleurs; ne tracez jamais de lignes verticales; laissez plutôt des espaces supplémentaires.

Indiquez les renvois dans les tableaux par des minuscules suscrites et placez les renvois au bas du tableau.

Placez les tableaux à la suite des références bibliographiques.

A l'endroit où le tableau est mentionné pour la première fois, indiquez dans la marge "Tableau — près d'ici."

Remarquez que les *tableaux dans le texte* ne sont pas *numérotés, sont dactylographiés avec le texte et ne re*quièrent que rarement des lignes horizontales (voir Appendice C).

Figures: Expédiez avec le manuscrit le *dessin original* et deux copies propres de chaque figure. Au coin inférieur gauche de chaque original et copie, inscrivez le nom de l'auteur et le numéro de la figure. De plus, annexez à chaque figure la légende qui lui est propre, pour fin d'identification. Dans le cas de photographies, dactylographiez l'information sur une lisière de papier que vous collerez au dos. N'écrivez pas à la main ou à la machine sur la photographie même. En plus, dactylographiez les légendes, dans l'ordre, sur feuille séparée, intitulée "Légendes des figures." Intercalez cette feuille à la suite du texte.

A l'endroit où chaque figure est mentionnée pour la première fois, inscrivez en marge "Fig. — près d'ici."

Equations, formules et expressions mathématiques: Laissez trois espaces au-dessus et au-dessous des lignes renfermant des chiffres ou des lettres suscrits et souscrits, ou encore au-dessus et au-dessous d'équations et de formules. Placez chaque composante des différentes expressions dans la position qui lui est propre (voir Appendice D).

Indiquez clairement tous les symboles. Epelez en marge les lettres grecques, la première fois qu'elles apparaissent. Faites une distinction entre la lettre l et le chiffre *un*, et entre la majuscule O et le chiffre *zéro*. Insérez de la même façon toute autre note explicative.

Références: Vérifiez le texte afin de vous assurer que toutes les références apparaissant dans la liste bibliographique sont bien mentionnées dans le texte. Dactylographiez à double interligne dans le style en usage dans le Journal (voir Appendice E). Les noms de revues sont abrégés suivant les *Biological Abstracts;* en cas de doute, écrivez le nom au long.

Orthographe: Une liste d'environ 100 mots communément employés dans les périodiques sur les pêches est donnée en Appendice F.

Appendices: On peut se procurer une copie des Appendices A à F sur demande au bureau du Directeur de la publication.

Structure, Functioning, and Management of Ecosystems

The First International Congress of Ecology

The Hague, The Netherlands

September 8–14, 1974

The main purpose of the Congress will be to bring together ecologists from all disciplines to discuss unifying concepts. Themes will be:

— Flow of energy and matter between trophic levels
— Comparative productivity in ecosystems
— Diversity, stability, and maturity in natural ecosystems
— Diversity, stability, and maturity in ecosystems influenced by human activities
— Strategies for management of natural and man-made ecosystems
— Significance of ecological principles for society

A number of special symposia will be held (partly organized by the International Biological Programme).

For further information contact:

Secretariat First International Congress of Ecology
P.O. Box 9000
The Hague
The Netherlands

Structure, fonctionnement et gestion des écosystèmes

Premier Congrès international sur l'écologie

La Haye (Pays-Bas)

Du 8 au 14 septembre 1974

Le but principal du Congrès est de réunir des écologistes de toutes les disciplines pour discuter de principes d'unification. Les thèmes en seront:

— Flux d'énergie et de matière entre les niveaux trophiques;
— productivité comparative dans les écosystèmes;
— diversité, stabilité et maturité dans les écosystèmes naturels;
— diversité, stabilité et maturité dans les écosystèmes influencés par les activités humaines;
— stratégies de la gestion des écosystèmes naturels et artificiels; et
— signification des principes écologiques pour la société.

On tiendra également un certain nombre de colloques spéciaux (organisés en partie par le Programme biologique international).

Pour plus de renseignements, écrire à l'adresse suivante:

Secrétariat, Premier Congrès international sur l'écologie
C.P. 9,000
La Haye
Pays-Bas

The First National Bass Symposium

February 3–6, 1975

Camelot Inn, Tulsa, Oklahoma, USA

The overall purpose for the Symposium is to develop a state-of-the-art assessment of current knowledge about the biology and management of America's most popular game fish — the so-called "black bass." The Symposium will also consider probable future management trends and suggest lines for future research.

While complete registration information will not be available until early next year, we urge you to plan now to be part of this historical meeting. Both the scientific and sportfishing communities have shown great enthusiasm for this unique undertaking. A large turnout is assured and we want your attendance and active participation.

For further information contact:

Richard Stroud (Chairman)
Executive Vice President
Sport Fishing Institute
608 13th St., NW (Suite 801)
Washington, D.C. 20005, USA

Premier symposium national sur l'achigan

du 3 au 6 février 1975

Camelot Inn, Tulsa (Oklahoma, E.-U.)

L'objectif principal du symposium est d'établir l'état actuel des connaissances sur la biologie et la gestion de l'une des espèces de poisson gibier les plus recherchées d'Amérique, l'achigan (black bass). Le symposium étudiera aussi les tendances éventuelles de sa gestion dans l'avenir et proposera des sujets de recherche.

Tous les renseignements concernant l'inscription ne seront pas disponibles avant le début de l'année prochaine. Nous vous prions donc de prévoir dès maintenant votre participation à cette réunion historique. Les pêcheurs sportifs et les scientifiques ont fait preuve d'un grand enthousiasme à l'égard de cette initiative unique. Nous attendons un nombre considérable de participants et nous comptons sur votre présence et votre participation active.

Pour d'autres renseignements, communiquez avec:

M. Richard Stroud (président)
Vice-président administratif
Sport Fishing Institute
608, 13^{e} rue, NW (suite 801)
Washington (D.C.) 20005, E.-U.

MISCELLANEOUS SPECIAL PUBLICATION 22 PUBLICATION DIVERSE SPÉCIALE 22

The Algal Bowl

Lakes and Man

J. R. VALLENTYNE

This is a book for nonspecialists about lakes and how they are affected by nutrients derived from human activities (man-made eutrophication). While the central theme of the book is that phosphorus is the key to the control of man-made eutrophication, an analysis of ultimate causes shows the need to control demophoric (population × technological) growth. A list of scientific terms and definitions; an appendix with an updating of events to 1974, suggestions for additional reading, and a sequence of tables and figures for the scientifically inclined reader are included.

Cet ouvrage, préparé à l'intention des non-spécialistes, traite des lacs et de la façon dont ils sont affectés par les apports de matières nutritives découlant des activités humaines (eutrophisation due à l'homme). Alors que le thème central de l'ouvrage porte sur le phosphore en tant que clé du contrôle de l'eutrophisation due à l'homme, une analyse des causes ultimes fait ressortir la nécessité de contrôler la croissance démophorique (population × technologie). Nous donnons une liste de termes scientifiques et définitions, une chronologie des événements jusqu'à 1974 en annexe, des références pour lectures supplémentaires et enfin une série de tableaux et de figures pour le lecteur à tournure d'esprit scientifique.

Canada: $3.00 *186 pages*

Other countries/Autres pays: $3.60

Available by mail from Information Canada, Ottawa K1A 0S9, and at the following Information Canada bookshops:

Halifax: 1683 Barrington Street
Montreal: 640 St. Catherine Street West
Ottawa: 171 Slater Street
Toronto: 221 Yonge Street
Winnipeg: 393 Portage Avenue
Vancouver: 800 Granville Street

Please make cheques and money orders payable to the Receiver General of Canada. Advance payment is required.

En vente à Information Canada à Ottawa K1A 0S9, et dans les librairies d'Information Canada:

Halifax 1683, rue Barrington
Montreal 640 ouest, rue Ste-Catherine
Ottawa 171, rue Slater
Toronto 221, rue Yonge
Winnipeg 393, avenue Portage
Vancouver 800, rue Granville

Payable à l'avance. Faire les chèques et les mandats payables à l'ordre du Receveur général du Canada.

Journal of the Fisheries Research Board of Canada

Volume 31, No. 5, May 1974 JFRBAK31(5)499–1021(1974)

Editor's Foreword **J. C. Stevenson** 499

Introduction to limnology in Canada **H. H. Harvey and G. H. Geen** 501–504

Lakes — the vital water resource in Canada **J. P. Bruce** 505–512

Limnology and education in the next decade **J. R. Vallentyne** 513–519

Impact of recent economic growth and industrial development on the ecology of Northwest Miramichi Atlantic salmon (*Salmo salar*) **P. F. Elson** 521–544

Benthos and allochthonous organic matter in streams **H. B. N. Hynes, N. K. Kaushik, M. A. Lock, D. L. Lush, Z. S. J. Stocker, R. R. Wallace, and D. D. Williams** 545–553

Limnological conditions in five small oligotrophic lakes in Terra Nova National Park, Newfoundland **J. J. Kerekes** 555–583

Physical and chemical limnology of Char Lake, Cornwallis Island (75° N lat.) **D. W. Schindler, H. E. Welch, J. Kalff, G. J. Brunskill, and N. Kritsch** 585–607

Benthic photosynthesis and respiration in Char Lake **H. E. Welch and J. Kalff** 609–620

Phytoplankton production in Char Lake, a natural polar lake, and in Meretta Lake, a polluted polar lake, Cornwallis Island, Northwest Territories **J. Kalff and H. E. Welch** 621–636

Production of zooplankton in Char Lake **F. H. Rigler, M. E. MacCallum, and J. C. Roff** 637–646

Eutrophication in the high arctic — Meretta Lake, Cornwallis Island (75° N lat.) **D. W. Schindler, J. Kalff, H. E. Welch, G. J. Brunskill, H. Kling, and N. Kritsch** 647–662

The morphoedaphic index, a fish yield estimator — review and evaluation **R. A. Ryder, S. R. Kerr, K. H. Loftus, and H. A. Regier** 663–688

Some aspects of Great Lakes physics of importance to biological and chemical processes **F. M. Boyce** 689–730

A summary and comparison of nutrients and related water quality in lakes Erie, Ontario, Huron, and Superior **H. F. H. Dobson, M. Gilbertson, and P. G. Sly** 731–738

A comparative review of phytoplankton and primary production in the Laurentian Great Lakes **R. A. Vollenweider, M. Munawar, and P. Stadelmann** 739–762

Benthic macroinvertebrates of the St. Lawrence Great Lakes **D. G. Cook and M. G. Johnson** 763–782

Zooplankton of the St. Lawrence Great Lakes — species composition, distribution, and abundance **N. H. F. Watson** 783–794

Review of geological research as it relates to an understanding of Great Lakes limnology **P. G. Sly and R. L. Thomas** 795–825

Changes in the fish species composition of the Great Lakes **W. J. Christie** 827–854

Crustacean plankton communities of 340 lakes and ponds in and near the National Parks of the Canadian Rocky Mountains **R. S. Anderson** 855–869

Factors affecting sockeye salmon (*Oncorhynchus nerka*) growth in four lakes of the Fraser River system **J. C. Goodlad, T. W. Gjernes, and E. L. Brannon** 871–892

Marion Lake (IBP) — from bacteria to fish **K. J. Hall and K. D. Hyatt** 893–911

Effects of hydroelectric development in western Canada on aquatic ecosystems **G. H. Geen** 913–927

Trout production in prairie ponds **G. H. Lawler, L. A. Sunde, and J. Whitaker** 929–936

Experimental Lakes area: whole-lake experiments in eutrophication **D. W. Schindler and E. J. Fee** 937–953

Recent limnological studies of Okanagan Basin lakes and their contribution to comprehensive water resource planning **J. G. Stockner and T. G. Northcote** 955–976

A review of research on the limnology of West Blue Lake, Manitoba **F. J. Ward and G. G. C. Robinson** 977–1005

Studies of northern Alberta lakes and their fish populations **M. J. Paetz and K. A. Zelt** 1007–1020

Coming next month/A paraître le mois prochain 1021

Guide to Authors and Typists/Guide des auteurs et Guide pour les secrétaires d'auteurs *i–iv*

INFORMATION CANADA, OTTAWA, 1974